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COVER IMAGE

Front cover: Figure 19 (page 83) California leaf-nosed bat, *Macrotus californicus* (photo by J. Scott Altenbach).
Back cover: Figure 33 (above) (page 158) Cave myotis, *Myotis velifer* (photo by J. Scott Altenbach). Figure 3 (below) (page 14) Red fruit bat, *Stenoderma rufum* (photo by Michael Gannon).

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United States Bat Species of Concern: A Synthesis

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In 1994, the federal government designated 24 species or subspecies of bats in the United States (U.S.) and its territories as Category 2 candidates for listing as Endangered or Threatened under the U.S. Endangered Species Act. Category 2 was eliminated in 1996, but taxa previously receiving this designation were informally considered "species of concern." Various state and federal agencies and conservation organizations subsequently assigned bat species of concern to more formal conservation categories. Some of the original 24 taxa designated as Category 2 candidates in 1994 were later listed as Endangered, whereas others were subject to refinements in knowledge of their taxonomy and distribution. The remaining 20 species of bats have been the subjects of increased research efforts over the past two decades, and are the focus of this review. Two species occur in the U.S. Territories. All of the 18 mainland species ranges include areas west of the Mississippi River (15 are found primarily in western states), and 13 occur in California (72% of the 18 mainland species). In this review, we provide a comprehensive summary of the literature pertinent to the conservation designations, systematics, distribution, habitats, relative abundance, foraging, diet, roosting ecology, population ecology, and management of each of these 20 species. The species of concern are distributed among four families of bats. The Samoan flying fox (*Pteropus samoensis*) belongs to the Old-World family, Pteropodidae. The California leaf-nosed bat (*Macrotus californicus*), red fruit bat (*Stenoderma rufum*), and Mexican long-tongued bat (*Choeronycteris mexicana*) are members of the New World family, Phyllostomidae. Three species belong to the cosmopolitan family Molossidae: the greater bonneted bat (*Eumops perotis californicus*), Underwood's bonneted bat (*Eumops underwoodi*), and the big free-tailed bat (*Nyctinomops macrotis*). Most bat species of concern are in the globally distributed family Vespertilionidae: Townsend's big-eared bat (*Corynorhinus townsendii*), Rafinesque's big-eared bat (*C. rafinesquii*), spotted bat (*Euderma maculatum*), Allen's big-eared bat (*Idionycteris phyllotis*), southeastern myotis (*Myotis austroriparius*), western small-footed myotis (*M. ciliolabrum*), long-eared myotis (*M. evotis*), eastern small-footed myotis (*M. leibii*), Arizona myotis (*M. occultus*), fringed myotis (*M. thysanodes*), cave myotis (*M. velifer*), long-legged myotis (*M. volans*), and Yuma myotis (*M. yumanensis*). An impressive amount of knowledge has accumulated about these species since their informal designation as species of concern, but this knowledge is unevenly distributed. Comparatively little research has been conducted on the Samoan flying fox and the red fruit bat over the past decade in tropical territories, nor on the Mexican long-tongued bat and Underwood's bonneted bat in the southwestern U.S. Within temperate regions of the U.S., habitat use of two eastern species that roost in hollow trees or caves (southeastern myotis and Rafinesque's big-eared bat) has been the focus of much research, as have aspects of the biology of cave-roosting and tree-roosting western species, particularly where information about management of forests, caves, and abandoned mines can be used to benefit bat conservation. Comparatively less information has accrued about species that roost in rock crevices and high on cliff faces. Other major gaps in information are also identified. We anticipate that this review will help guide future research and conservation efforts directed at the bat species of concern.

KEYWORDS: Bats, Chiroptera, *Choeronycteris*, Conservation, *Corynorhinus*, Ecology, *Eumops*, *Idionycteris*, *Macrotus*, *Myotis*, *Nyctinomops*, *Pteropus*, *Stenoderma*.

In her landmark early publication on the bats of California, Hilda Grinnell (1918) made note of the desirability to protect and conserve bat populations throughout the United States (U.S.) and cited conservation efforts that extended back to the early 1800s. Mounting concern for the conservation of bat populations in the U.S. and territories has been expressed repeatedly in other technical publications since at least the middle of the last century (for example, Mohr, 1952, 1972; Manville, 1962; Barbour and Davis, 1969; Cockrum, 1969, 1970). The Indiana bat (*Myotis sodalis*) was one of the 14 taxa of mammals placed on the original U.S. endangered species list in 1967 (Udall, 1967). Other species of bats were subsequently added to this list, and by 1994 increasing concern for the status of bat populations was reflected in the designation of 24 species or subspecies of bats among a broader group of animals considered to be Category 2 candidates for federal listing under the U.S. Endangered Species Act of 1973 (U.S. Fish and Wildlife Service, 1994; Table 1). Category 2 candidates were defined as "taxa for which information…indicates that proposing to list as endangered or threatened is possibly appropriate, but for which persuasive data on biological vulnerability and threat are not currently available to support proposed rules" (U.S. Fish and Wildlife Service, 1994:58983).

SPECIES OF CONCERN

Category 2 candidate species were not provided any official protection, and in 1996 the U.S. Fish and Wildlife Service discontinued the use of a Category 2 candidate status for all such previously designated animals and plants. Instead they noted "the Service remains concerned about

TABLE 1. Species or subspecies of bats in the U.S. and territories originally designated as Category 2 candidates for listing under the Endangered Species Act in 1994 (U.S. Fish and Wildlife Service, 1994). In 1996, the U.S. Fish and Wildlife Service eliminated Category 2 but considered all species of plants and animals formerly categorized as such to be "species of concern" (U.S. Fish and Wildlife Service, 1996a, 1996b). CNMI = Commonwealth of the Northern Mariana Islands. Bat names have been updated.

Species or Subspecies of Bat	General Distribution in United States
Choeronycteris mexicana, Mexican long-tongued bat	Arizona, New Mexico
Corynorhinus rafinesquii, Rafinesque's big-eared bat	Southeastern and south-central U.S.
Corynorhinus townsendii pallescens, Pale Townsend's big-eared bat	Western U.S. (inland populations)
Corynorhinus townsendii townsendii, Pacific Townsend's big-eared bat	Western U.S. coast
Emballonura semicaudata, Pacific sheath-tailed bat	Pacific islands (several island groups)
Euderma maculatum, Spotted bat	Western U.S.
Eumops perotis californicus, Greater bonneted bat	West coast and southwestern U.S.
Eumops underwoodi, Underwood's bonneted bat	Arizona
Idionycteris phyllotis, Allen's big-eared bat	Southwestern U.S.
Macrotus californicus, California leaf-nosed bat	Southwestern U.S.
Myotis austroriparius, Southeastern myotis	Southeastern and south-central U.S.
Myotis ciliolabrum, Western small-footed myotis	Western U.S.
Myotis evotis, Long-eared myotis	Western U.S.
Myotis leibii, Eastern small-footed myotis	Central and eastern U.S.
Myotis occultus, Arizona myotis	Southwestern U.S.
Myotis thysanodes, Fringed myotis	Western U.S.
Myotis velifer, Cave myotis	Southwestern U.S.
Myotis volans, Long-legged myotis	Western U.S.
Myotis yumanensis, Yuma myotis	Western U.S.
Nyctinomops macrotis, Big free-tailed bat	Southwestern U.S.
Pteropus mariannus mariannus, Mariana fruit bat	CNMI population
Pteropus mariannus paganensis, Pagan Mariana fruit bat	CNMI (Pagan population)
Pteropus samoensis samoensis, Samoan flying fox	American Samoa
Stenoderma rufum, Red fruit bat	Puerto Rico, U.S. Virgin Islands

these species, but further biological research and field study are needed to resolve the conservation status of these taxa. Many species of concern will be found not to warrant listing…Others may be found to be in greater danger of extinction than some present candidate taxa" (U.S. Fish and Wildlife Service, 1996a:7597). The Category 2 candidate species of bats designated in 1994 thus became known informally as "Bat Species of Concern". Many of these species of bats were at that time or later also categorized as sensitive species by other state and federal land management agencies and conservation organizations, as encouraged by the U.S. Fish and Wildlife Service (1996b). Our objectives in this report are to summarize the current conservation status of these former Category 2 candidate species of bats and to summarize pertinent biological information on these taxa, particularly information that has become available due to research in the ensuing two decades since 1996.

CHANGES IN THE FEDERAL STATUS OF BATS IN THE UNITED STATES AND TERRITORIES

During the ensuing two decades (1967–1988) since placing the Indiana bat on the list of U.S. endangered species, eight additional species or subspecies of bats were designated as endangered (Table 2). This includes the categorization of the Guam population of the Mariana fruit bat (*Pteropus mariannus mariannus*) as endangered in 1984 (U.S. Fish and Wildlife Service, 1984), a population and taxon subsequently downlisted as threatened together with the population in the Commonwealth of the Northern Mariana Islands in 2005 (U.S. Fish and Wildlife Service, 2005). No other taxa of bats were added to the list of endangered or threatened species in the U.S. and territories for the 25 years following 1988, but this changed during 2013–2016 when another four taxa were added (Table 2). The Florida bonneted bat (*Eumops floridanus*; elevated to full species taxonomic status by Timm and Genoways [2004] since the 1994 designation as a Category 1 candidate subspecies) was listed as endangered due to multiple factors: habitat loss, habitat degradation and modification, as well as threats due to small population size, restricted range, few colonies, low fecundity, and relative isolation (U.S. Fish and Wildlife Service, 2013a). The Mariana subspecies of the Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*) was listed as endangered in 2015, in part because several updated studies (for example, Gorresen et al., 2009; Wiles et al., 2011; Valdez et al., 2011; Oyler-McCance et al., 2013) confirmed its need for strict protection due to: reduction from a larger, multi-island distribution to its present occurrence only on the tiny island of Aguiguan; an apparent specialization for native limestone forest as foraging habitat, loss of which has been due to over-utilization by feral goats and encroachment by exotic vegetation; and risk of future declines due to typhoons and predation (U.S. Fish and Wildlife Service, 2015a). The northern long-eared bat was listed as threatened in 2015 (Table 2) due to very recent and dramatic population declines caused by the fungal disease white-nose syndrome (U.S. Fish and Wildlife Service, 2015b). In 2016, the South Pacific subspecies of the Pacific sheath-tailed bat (*Emballonura semicaudata semicaudata*) also was designated as endangered on American Samoa as well as on Fiji, Samoa, Tonga, and Vanuatu. Reasons for endangerment included habitat loss from deforestation, mortality from non-native predators, disturbance of caves used as roosts, low numbers, vulnerability to catastrophic events, and breakdown of the metapopulation structure due to increasing isolation of subpopulations (U.S. Fish and Wildlife Service, 2016). Twenty former Category 2 candidate taxa remained among the original 24 species and subspecies of concern given these changes (two western subspecies of Townsend's big-eared bat [Table 1] considered as a single species here, coupled with the recognition of the Commonwealth of the Northern Mariana Islands and Guam population of the Mariana fruit bat as threatened, the lack of evidence for the

TABLE 2. Species and subspecies of bats within the United States and its territories listed as endangered or threatened under the U.S. Endangered Species Act of 1973 or its forerunner legislation. Species are listed in chronological order of designation. *Pteropus tokudae* is considered extinct (Bonaccorso et al., 2008).

Species	Common Name	Designation	Year of Listing	References
Myotis sodalis	Indiana bat	Endangered	1967	Udall (1967)
Lasiurus semotus	Hawaiian hoary bat	Endangered	1970	Gottschalk (1970)
Myotis grisescens	Gray bat	Endangered	1976	U.S. Fish and Wildlife Service (1976)
Corynorhinus townsendii ingens	Ozark big-eared bat	Endangered	1979	U.S. Fish and Wildlife Service (1979)
Corynorhinus townsendii virginianus	Virginia big-eared bat	Endangered	1979	U.S. Fish and Wildlife Service (1979)
Pteropus mariannus mariannus	Mariana fruit bat or Fanihi	Endangered/ Threatened[1]	1984/2005	U.S. Fish and Wildlife Service (1984, 2005)
Pteropus tokudae	Little Mariana fruit bat	Endangered	1984	U.S. Fish and Wildlife Service (1984)
Leptonycteris curasoae yerbabuenae	Lesser long-nosed bat	Endangered[2]	1988	U.S. Fish and Wildlife Service (1988)
Leptonycteris nivalis	Mexican long-nosed bat	Endangered	1988	U.S. Fish and Wildlife Service (1988)
Eumops floridanus	Florida bonneted bat	Endangered	2013	U.S. Fish and Wildlife Service (2013a)
Emballonura semicaudata rotensis	Pacific sheath-tailed bat (Mariana subspecies)	Endangered	2015	U.S. Fish and Wildlife Service (2015a)
Myotis septentrionalis	Northern long-eared bat	Threatened	2015	U.S. Fish and Wildlife Service (2015b)
Emballonura semicaudata semicaudata	Pacific sheath-tailed bat (South Pacific subspecies)	Endangered	2016	U.S. Fish and Wildlife Service (2016)

[1] Originally designated endangered on Guam in 1984; down-listed to threatened on Guam and designated as threatened throughout the Commonwealth of the Northern Mariana Islands in 2005 with recognition that one population occurred in both entities

[2] Proposed for de-listing due to recovery January 6, 2017 (U.S. Fish and Wildlife Service, 2017).

existence of a Pagan subspecies of the Mariana fruit bat [U.S. Fish and Wildlife Service, 2005], and the listing of the Pacific sheath-tailed bats as endangered). The species accounts in this publication pertain to these 20 species.

A NEED FOR CONSERVATION AND RESEARCH FOR U.S. BATS

The dynamics of bat populations are more akin to those of larger, long-lived mammals than of other small mammals. Bat populations tend to be more susceptible to long-term declines and are slower to recover from population losses than similarly sized mammals. Unlike many other small mammals, bats have low reproductive rates (usually one young per litter once annually, with variability in pregnancy rates in any given year) and most importantly, require high annual survival of adults to maintain stable populations (for example, O'Shea et al., 2011c). Unlike many other long-lived mammals, numerous species of bats require special and spatially limited seasonal conditions for roosting that force them to gather in aggregations when rearing young and when hibernating in winter, rendering these aggregations very susceptible to mortality, disturbance, or loss of habitat. Bats are important components of national biodiversity and are economically important as consumers of insect pests nationwide, as pollinators of plants in the southwestern states, and as dispersers of seeds in the tropical territories (for example, Boyles et al., 2011; Fenton and Simmons, 2015; Maine and Boyles, 2015; Wiederholt et al., 2013). Forty-seven species of bats are found in the 50 United States (Bradley et al., 2014; excluding rare and anomalous occurrences), with other species found in the U.S. territories. Within the 50 U.S. states, eight taxa (including subspecies of big-eared bats) are threatened or endangered (Table 2), which together with 18 species of concern within the states encompass more than half of all U.S. species of bats exclusive of the territories.

The need for conservation and research efforts for bats has been underscored over the past 10 years by the emergence of two major, unforeseen threats acting on U.S. bat mortality: the growth in the wind energy industry causing increases in bat deaths at operating turbines, and the emergence of white-nose syndrome, the fungal disease resulting in massive die-offs at bat hibernacula (for example, Frick et al., 2010a; Turner et al., 2011). This mortality is unprecedented globally (O'Shea et al., 2016a). These relatively new issues are superimposed on several more long-standing chronic problems that have confronted U.S. bat populations for decades.

Objectives, Organization, and Content of This Publication

This report is targeted for natural resource managers who may have limited knowledge about bats and the issues impacting their populations, and for researchers who may be initiating work on particular topics or species. The species accounts provide a summary of knowledge about each of the 20 former Category 2 candidate species of bats (species of concern), allowing the reader the opportunity to identify and consult the many cited references that give further details. This section does not provide accounts for species or subspecies that are currently listed as endangered or threatened under the U.S. Endangered Species Act of 1973 (Table 2). Those species are the subjects of detailed recovery plans and other documents that can be found elsewhere.

Each account is divided into sub-sections regarding aspects of the species biology that are fundamental for understanding their conservation needs. Our intention in developing these accounts is to provide extensive summaries of much of the scientific literature pertinent to the subsection topics as published through much of 2017, but readers should consult the cited original papers for further details and to verify our interpretations.

The species account subsections and the material they are intended to summarize begin with the scientific and common names as recognized by Simmons (2005). These are followed by a summary of **Conservation Status** information that includes status designations by (1) various national and international agencies and organizations, and (2) each of the 50 states as well as pertinent U.S. territories. A physical **Description** of the species follows, highlighting unique features and possible distinguishing characteristics (if in doubt, readers should consult more definitive sources for additional details for identification). The description is followed by a section on **Distribution and Systematics** that provides a description of regions where the species can occur as well as a coarse-scale distribution map, and summary information on taxonomy and nomenclature. The distribution maps of bats were made with publicly available distribution information from the National Atlas of the United States (U.S. Geological Survey, 2017). Distributions of all organisms are dynamic and imprecisely known. The maps are provided to convey the general range of places a species might be encountered during one or more seasons. They are not intended to be precise representations of areas where species consistently occur and may not include anomalous records or outliers. The information on systematics, taxonomy, and nomenclature is not trivial because the literature for some of these species includes different scientific names used over the years, and use of these names can be confusing even to a specialist; indeed some names may still be in flux, particularly as new molecular genetic studies of evolutionary relationships continue to cause refinements in systematic treatments of bats. This section also provides the reader with other common names found in the literature, as well as interesting information about the etymology (Latin or Greek meanings) of the scientific name or about the person for whom a species might be named (patronym or eponym; for example, Townsend, Leib, and others).

The section on **Habitats and Relative Abundance** gives details regarding habitats utilized by the species (**Roosting Habits** are provided in a separate section, see below). The description of habitats utilized includes general information on elevations, physiographic and geologic features, and vegetation types as studied in various parts of the species distribution. For ease of navigation by the reader, this section is usually hierarchically organized by geographic regions and then state or province. Although there are many ecological classifications of vegetation zones available, we limit our use to general categorizations or those provided by original authors, and recommend that readers consult the original works as well as recent sources on vegetation classification schemes for greater details. This section also provides findings on the relative abundance of species of concern as available from published bat community surveys using mist nets or in some cases echolocation detectors. Information on relative abundance of wildlife in general can be difficult and sometimes inappropriate to evaluate (for example, Anderson, 2001), and inferences in the case of bats should be strongly qualified by the many known (and perhaps many still unknown) biases inherent in such surveys.

Biases associated with capture surveys can include the availability of preferred roosting sites in an area; the basis for capture data (such as mist nets, harp traps, echolocation detectors, and their placement); species differences in maneuverability and susceptibility to capture (which with mist netting may vary according to the availability of water for drinking or with body mass when pregnant); or investigator bias when seeking out particular species while conducting surveys. Biases associated with acoustic surveys include differences in intensity, detectability, and uniqueness of echolocation pulses among species and an inability to count individual bats. Nonetheless, more accurate and precise methods for estimating true abundance of bats have been elusive (O'Shea and Bogan, 2003; Loeb et al., 2015). We therefore include information about relative abundance from surveys because it may have utility in qualitatively judging the possible rarity or commonness of a particular species of concern in surveyed habitats, landscapes, or regions of specific interest. It may also help guide future research efforts on habitat use by bats. The reader should also bear in mind that species abundances in bat community surveys follow general, often log-normal, patterns seen in many other biotic communities (Magurran, 2004). These patterns often consist of many individuals of a few common species, with fewer individuals distributed with decreasing frequency across a larger number of less common species (for additional background on patterns of diversity and abundance in bats see Kingston, 2009). Due to the sparse or geographically variable nature of habitat and relative abundance information available on most bat species of concern, we refrain from generalizing prior observations through tabulation or other types of synthesis. Instead most observations are presented in narrative form, with the hope that consistent patterns eventually will take shape and encourage the scientifically vital next steps of hypothesis formulation and testing regarding causal factors affecting differential use of habitats by bats.

The section on **Foraging and Dietary Analysis** summarizes published observations and more rigorous research (where available) on the foraging habits of each species, including dietary components ascertained through analyses of feces or stomach contents.

The section **Roosting Habits** summarizes current knowledge on general roosting habits, winter roosts, warm season roosts, night roosts, and other aspects of each species' roosting ecology. Different species of bats can be very specialized or generalized in their choice of roosts, but availability of suitable roosts can be a limiting factor for some species in particular habitats (for example, Kunz, 1982; Kunz and Lumsden, 2003), with the diversity of available roosting substrates influencing U.S. regional species diversity of bats (for example, Humphrey, 1975). The section on roosting habits reviews the literature on generalized knowledge of roosting habits for each species of concern, including: substrates used as roosts (for example, rocks, trees, caves); sizes and composition of roosting groups; seasonal use of roosts in spring and autumn, summer, and winter; and functions of roosts including night roosts, swarming or staging sites, maternity (nursery) colonies, or hibernacula. Information is also provided on "roost-switching", wherein colonies or individuals may move among roosts with varying frequency (Lewis, 1995). The section also includes summaries of specialized information derived from more intensive modern studies, such as those that utilize radio telemetry coupled with quantitative habitat models to ascertain important features of roosts versus randomly selected structures or landscape features.

Two main sections round out the species accounts. **POPULATION ECOLOGY** reviews fundamental information pertinent to species life history and demographic traits, including reproduction, mortality factors, population trends, or population genetics that may be of interest for future studies such as those aimed at modeling population dynamics or assessment of trends. Life history traits include subheadings with citation of published data regarding reproduction, including litter size (sometimes based on surprisingly scant sample sizes), and proportion of adult females that are reproductive (natality or fecundity rates) each year. The latter can be quite variable depending on ecological conditions during the season of sampling and where the samples are taken. Higher rates are typical if bats are sampled at maternity colonies. Lower rates may prevail if females are sampled away from maternity colonies because non-reproductive females may not use maternity roosts, and in some species and regions non-reproductive females will use different habitats (for example, Cryan et al., 2000). Other life-history variables such as adult survival, juvenile survival, or age-specific female reproductive rates (one-year old females may have lower reproductive rates than older adults; for example, Davis and Barbour, 1970; O'Shea et al., 2010) are not available for most species of bats but are provided in the few cases where they have been estimated. Mortality factors are also given, along with other relevant or interesting information such as sex ratios and maximum reported longevities. The final two subheadings in the **POPULATION ECOLOGY** section include the limited available information on population trends and population genetics. Monitoring of trends in bat populations has suffered estimation and analytical shortcomings (for example, O'Shea and Bogan, 2003), but new count methods and occupancy-based surveys continue to be developed and implemented (Loeb et al., 2015; see also individual accounts). Included under trend information are reviews of studies that provide occupancy and detectability estimates, and reviews of case studies of trials in which other novel sampling methods have been carried out. This section also reviews compilations of observations that allow more qualitative appraisals of population trend. Information on population genetics emphasizing genetic diversity are given in the section on **POPULATION ECOLOGY** as available.

A section on **MANAGEMENT PRACTICES AND CONCERNS** follows, with results of specific studies aimed at providing management recommendations, or a summary of major conservation concerns that the literature indicates require addressing. A final section, **NOTES AND COMMENTS**, appears in some accounts. This section adds brief information that may be unusual or of general interest that is not described in the other sections within that species account.

Species Accounts: The Territories

Pteropus samoensis — Samoan Flying Fox (Family Pteropodidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Listed in CITES Appendix I (Convention on International Trade of Wild Flora and Fauna, 2016). International Union for the Conservation of Nature (2017): Near Threatened.

Territorial Designation: American Samoa Department of Marine and Wildlife Resources (Utzurrum et al., 2006): Conservation Status II (High Priority), legally protected.

Description.— The Samoan flying fox (Fig. 1) has a dorsum that is generally dark brown interspersed with numerous long silver hairs, with a lighter colored mantle (Banack, 2001). The venter is various shades of brown with interspersed yellow hairs, the top of the head is pale yellow, and the mantle can be red, orange, or yellow (Flannery, 1995; Banack, 2001). However, individual variation in general coloration ranges from reddish brown to blackish gray (Banack, 2001). Forearm measurements range from about 125 to 155 millimeters, and body mass ranges 240 to 440 grams (including volant juveniles; Banack and Grant, 2003). These bats are sympatric with only one other fruit bat, the Pacific flying fox (*Pteropus tonganus*), and both are of similar size: adult Samoan flying foxes average 379 grams, whereas adult Pacific flying foxes average 428 grams (Banack, 1998). However, Pacific flying foxes have a black back, bright yellow mantle, and longer snout.

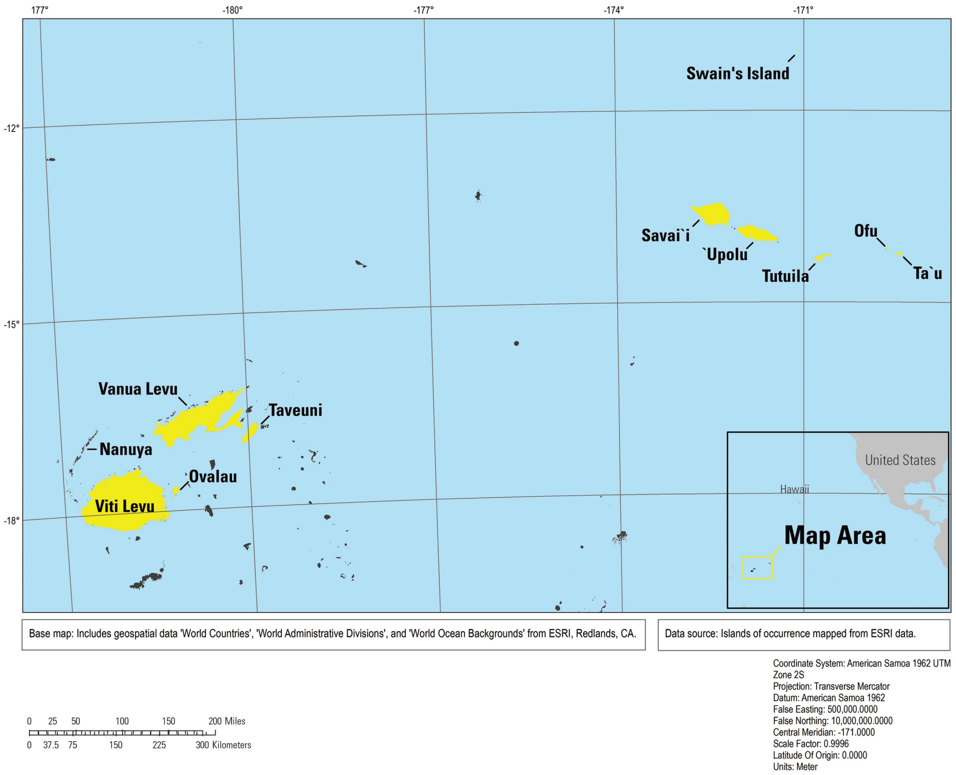
Figure 1. Samoan flying fox, *Pteropus samoensis* (photo by Frida Fjellström).

Distribution and Systematics.— In American Samoa, documented records exist for the Manu`a Islands (Ta`u and Ofu), Swain's Island, and Tutuila (Fig. 2; Flannery, 1995). In the independent nation of Samoa, this bat is known from Savai`i and `Upolu, and in Fiji from Nanuya, Ovalau, Taveuni, Vanua Levu, and Viti Levu. Fossil records exist for the island of `Eua in Tonga, where it is now considered extinct (Flannery, 1995).

Two subspecies are recognized in the Pacific Islands, *Pteropus samoensis samoensis* from the Samoa Islands (the former Category 2 candidate in American Samoa) and *P. samoensis nawaiensis* from Fiji (Flannery, 1995; Banack, 2001). Banack (2001) provided a complete taxonomic synonymy of past scientific names applied to the Samoan flying fox. The generic name *Pteropus* stems from Greek words for "wing" and "foot". The specific epithet is based on geography. Other English common names are Samoa flying fox and Samoan fruit bat. The Samoan names are pe'a or pe'a vao.

Habitats.— Samoan flying foxes occupy mature primary rain forest. Details on foraging and roosting habitats are provided below.

Foraging and Dietary Analysis.— Samoan flying foxes feed on a variety of fruits, flowers, and leaves and forage during the day as well as during the night. Foraging areas of two bats



Base map: Includes geospatial data 'World Countries', 'World Administrative Divisions', and 'World Ocean Backgrounds' from ESRI, Redlands, CA.

Data source: Islands of occurrence mapped from ESRI data.

FIGURE 2. Approximate distribution of the Samoan flying fox, *Pteropus samoensis*. Islands where the species occurs are colored yellow. The islands of American Samoa are in the upper right, and include Tutuila, Ofu, Ta'u, and Swain's Island. The species is also found on islands of the independent nation of Samoa (islands of Savai'i and 'Upolo in the upper right), and in Fiji (islands of Vanua Levu, Taveuni, Ovalau, Viti Levu, and Nanuya in the lower left).

radio tracked in American Samoa covered two to eight square kilometers at night and one to two square kilometers during the day (Brooke, 2001). They are pollinators and dispersing agents for native trees and are considered to be generalists in feeding strategy. On Tutuila in American Samoa, Banack and Grant (2003) observed regular feeding on 20 species of plants, primarily fruits and flowers and to a lesser extent leaves; food items were typical of primary forest habitats. They observed foraging in daylight hours, mostly at dawn and in late afternoon and early evening. However, some nocturnal activity was also documented (Banack and Grant, 2003). Mid-day soaring was observed, and indications of male-female pair territoriality were noted, with suggested territory sizes of about two square kilometers and roosts of pairs centered along ridge tops (Banack and Grant, 2003).

On American Samoa (primarily Tutuila) and the island of Savaii in Samoa, 36 different plant species have been documented as sources of food, with many more species also likely to be utilized (Banack, 1998). These encompass a large proportion of the canopy-forming trees, including many endemics. Use of fruits from any one species of tree shifts by time of year. The three species most selected by Samoan flying foxes and Pacific flying foxes (diets of the two species could not always be separated) for fruits on Samoa are: *Planchonella samoensis, P. garberi*, and *Terminalia catappa*. However, many other species are also used, with the five most dominant being *Artocarpus altilus, Inocarpus fagifer, Palaquium stehlinii, Planchonella samoensis,* and *Syzygium ino-*

phylloides (Banack, 1998). The importance of flowers in the diet relative to fruit is not known, but several species of plants are used for nectar, pollen, or consumption of entire flowers, particularly at times when fruit resources are low. These may include *Erythina variegata, Freycinetia reinecki, Palaquium stehlinii, Planchonella samoensis,* and *Syzygium inophylloides* (Banack, 1998). Agricultural fruits may be utilized at some times of year, but fruits of primary forest trees are selected over those from agricultural forest or secondary forest, and *P. samoensis* shows lower use of agricultural plants than the sympatric *P. tonganus* on Samoa. This may be because the nutritional value of native fruits used in the diet of *P. samoensis* is higher than the nutritional value of agricultural fruits (Nelson et al., 2000a). Consumption of unripe fruit and leaves during dry seasons and after hurricanes may provide many key nutrients in amounts comparable to those found in ripe fruits (Nelson et al., 2000b). Plants utilized by the closely related *P. samoensis nawaiensis* for fruit and forage on Fiji are also highly valued by human residents for food, medicine, and other cultural uses (Scanlon et al., 2014).

Roosting Habits.— Mature primary forest is favored as roosting habitat as well as for foraging. Individual Samoan flying foxes can shift roost sites among trees within forest patches up to 12 times in a day; roost sites include branches in dead trees and at least eight species of living trees, with roosting branches typically from five to 20 meters above ground (Brooke et al., 2000). Roost trees are often located at the edges of cliffs or ridge-tops that allow good conditions for dropping into flight (Banack and Grant, 2003). Unlike many species of flying foxes, Samoan flying foxes do not form large colonies. They roost primarily as solitary individuals, pairs (most common), or in small groups (Pierson and Rainey, 1992). Brooke (1997, 2001) and Banack and Grant (2003) described roosting patterns. Most solitary individuals are adult males. Pairs can consist of male-female dyads from August to March or mothers and young from April to July. The largest roosting group consisted of a transitory aggregation of up to 60 bats of both sexes (Brooke, 1997, 2001). Dead branches in ridge-top trees exposed to sunlight are conspicuous roosts for single males, particularly in early daylight, but bats make nearby movements to other less-exposed branches when temperatures increase during the day or under windy and rainy conditions. Females and dependent young typically roost in the canopy under less-exposed conditions. Individuals may repeatedly use the same branch (Brooke, 2001). This species can be tolerant of people and human activity beneath their roost sites (Brooke et al., 2000).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Litter size is one in nearly all pteropid fruit bats (Pierson and Rainey, 1992; Racey and Entwistle, 2000). Female Samoan flying foxes can be observed carrying single young in all months of the year. However, observations with young peak in March through September, with most nonvolant young seen in June through August (Pierson et al., 1992, 1996a; Brooke, 2001). Copulations have been observed in September and October (Brooke, 2001). A study in 1992–1994 that included Tutuila reported diffusely seasonal reproduction, with a peak of births in May and June with no newborns in November through February, and volant young (who continue to suckle after becoming volant) first appearing in August (Banack and Grant, 2003). August and September weaning coincides with fruit production in an important food plant, *Syzygium inophylloides* (Banack and Grant, 2003). We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as natality, age at first reproduction, and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Impacts of predation, disease or parasitism on Samoan flying fox mortality are undocumented in American Samoa. In the Fiji Islands, fruit bats are a major prey item of peregrine falcons (*Falco peregrinus*; White et al., 1988) and are taken by barn owls (*Tyto alba*;

Grant and Banack, 1995). The Samoan flying fox is nocturnal on Fiji but is well known to be more diurnal in the Samoa Islands, and perhaps diurnality is facilitated by the absence of birds of prey.

Hunting and deaths as a result of cyclones impacting food availability and habitat structure are the major recognized mortality factors and have serious implications (see details under "Management Practices and Concerns" below). Monitoring of a limited number of roosting sites of *P. samoensis* in American Samoa before and after two cyclones showed continued occupancy. However, mortality of immature *P. samoensis* as a result of the cyclones appeared to be high (Pierson et al., 1996a). Craig et al. (1994) modeled population growth projections for a likely initial size of 400 Samoan flying foxes with no further hunting or hurricanes, and calculated that it would take from 13–40 years to reach a desirable size of 1,500 bats. If hunting continued at a rate considered typical, the population would likely decrease steadily or at best not achieve the desirable size for more than a century, even in the absence of catastrophic storms (but see section on "Management Practices and Concerns below).

Population Trend: According to Flannery (1995:289), "This beautiful flying-fox is still readily observed in many parts of Fiji, but it is now on the verge of extinction in parts of Samoa." A petition to the U.S. Fish and Wildlife Service to list the species as endangered prompted a series of field surveys beginning in the mid-1980's (Wilson and Engbring, 1992; Craig et al., 1994). Surveys were improved each year to result in an index based on standardized counts of daytime-active bats from a series of viewing stations (mean number of bats seen/size of viewing area/20–minute period for five replicate counts), primarily on Tutuila (Craig et al., 1994; Morrell and Craig, 1995). This index, which typically ranged from about six to eight from 1986 to 1990, dropped drastically to about 1.5 in 1991 and 1992 (Craig et al., 1994). This decline was attributable to damage from a severe hurricane in 1990. An approximation of population size for Tutuilla was calculated by multiplying the index by the total available suitable area and making somewhat arbitrary corrections for inactive (undetectable) bats, species misidentifications, and bats moving among survey areas. This index suggested that only about 200–400 *P. samoensis* remained on Tutuila after Hurricane Ofa (Craig et al., 1994), in comparison with a pre-Ofa estimate of less than 700 (Pierson et al., 1996a). Craig et al. (1994) noted that out of the four islands of Tutuila, Ta'u, Olosega, and Ofu, nearly 70% of the remaining population in 1992 occurred on Tutuila, and about 25% on Ta'u. A population size of 300–500 was suggested for Tutuila in the early 1990s (Banack and Grant, 2003). Additional surveys were conducted in 1995–1996 using somewhat different techniques, and in 1996 the number of *P. samoensis* on Tutuila was estimated at 854 (Brooke, 1997). However, arriving at population size or trend estimates for this species has been problematic due to the ad hoc nature and numerous changes in survey methods over time (Utzurrum et al., 2003), as well as recent recognition that on American Samoa many of these bats are active at night (Brooke, 2001; Banack and Grant, 2003). As a result, counts based on diurnal activity alone could be underestimates (Brooke, 2001). Population growth rate estimates based on a simple model have been made to assess the likely importance of mortality factors (Craig et al., 1994; see "Mortality" above).

Population Genetics: Analysis of mitochondrial D-loop and microsatellite nuclear DNA of Samoan flying foxes was conducted based on samples from American Samoa (Olosega, Ofu, and Tutuila), Fiji, and Samoa (Russell et al., 2016). Mitochondrial DNA from 19 bats in American Samoa showed high haplotype diversity and nucleotide diversity; observed heterozygosity at six microsatellite loci did not deviate from Hardy-Weinberg expectations (Russell et al., 2016). Genetic structuring among those islands sampled across American Samoa, Samoa, and Fiji was apparent from the mitochondrial DNA analysis but not from microsatellite nuclear DNA analysis, which revealed detectable genetic differences only among archipelagos rather than individual islands (Russell et al., 2016).

Management Practices and Concerns.— Daylight activity makes Samoan flying foxes vulnerable to human hunting (Banack and Grant, 2003). Shooting (including by sling-shot) has been a major concern. Cox (1983) reported that in the mountains of Tapatapao on Upolo Island the numbers taken by hunters dropped from 30 in 1979 to nine in 1980 and zero in 1981. Due to demand as a delicacy in Guam, exports of fruit bats (*P. samoensis* and *P. tonganus*) increased during the mid-1980's from 30 to 540 bats per year before 1983 to 1,632 bats exported in 1984 (Wiles, 1992). Commercial hunting and export of fruit bats from American Samoa was banned in 1986, and local hunting regulations instituted with bag-limits of seven per day, a three-month season, and prohibition of daytime hunting. This was followed by a Territorial government three-year ban on all hunting in 1992 (Craig et al., 1994), which may not have been well enforced (Pierson et al., 1996a). Major public education campaigns have taken place to help improve conservation of fruit bats in American Samoa (Daschback, 1990). Nonetheless, illegal hunting was not eliminated (Brooke et al., 2000). Population modeling by Craig et al. (1994) suggests that recovery is unlikely if hunting occurs at a rate considered typical. However, more recent observations suggest that estimates for model parameters may have been too conservative, and that closely managed hunting might even provide a tool for more effective population monitoring (Utzurrum et al., 2003).

Severe hurricanes (cyclones) superimposed a major impact over pressures from hunting. Hurricane Ofa in 1990 and Val in 1991 resulted in direct mortality, major alterations of habitat that included extensive defoliation of trees, and destruction of food plants in natural areas with subsequent starvation (Daschback, 1990; Craig and Syron, 1992). Fruit bats left forest habitats after Hurricane Ofa, the most severe storm since the early 1800's, and entered agricultural areas and villages in search of food, making them more susceptible to local hunting: the opportunistic harvest recorded on Tutuila in 1990 was extremely high (Daschback, 1990; Craig et al., 1994). However, the vast majority of these were Pacific flying foxes, not Samoan flying foxes (Pierson et al., 1996a). Unlike Pacific flying foxes, Samoan flying foxes were able to persist on leaves, petioles, and fleshy bracts of several storm-resistant plants immediately after the cyclones and were able to feed in closer proximity to roosts (Pierson et al., 1996a); foraging effort, however, increased after the cyclones (Grant et al., 1997).

Brooke (2001) concluded that the long-term survival of Samoan flying foxes on American Samoa will depend on the preservation of continuous, relatively undisturbed forest tracts and limited hunting. Rain forest reserves have been established that help protect the Samoan flying fox in the nation of Samoa, and populations in American Samoa also occur in protected zones (including *de facto* reserves on private land). The number of roost sites for these bats increased or remained stable in reserve areas after the damage from cyclones, but generally decreased outside of reserves (Pierson et al., 1996a). Although their adequacy for long-term survival of Samoan flying fox populations has been questioned, the two reserves in Samoa (totaling 10,000 ha) are thought to be sufficient for short-term maintenance of small populations of these bats even after severe storms, in part due to undamaged forest protected by volcanic craters; design of future reserves should include areas with high topographic complexity that will be more likely to survive storms with vegetation intact (Pierson et al., 1996a). Based on mitochondrial DNA analysis, it has been suggested that inter-island dispersal of Samoan flying foxes may be low, and that should populations become extinct on individual islands in the future active translocation of individuals may be a needed management strategy (Russell et al., 2016).

Samoan flying foxes and the more widespread Pacific flying foxes have co-existed with islanders for thousands of years, and play a conspicuous role in tradition and folklore (Sinavaiana and Enright, 1992). Despite tolerance of some human activities (Brooke et al., 2000), monitoring of roost sites on Alva Ridge in American Samoa suggests abandonment coincidental to increased use by recreational four-wheel drive vehicles (Pierson et al., 1996a). Banack and Grant (2003) also note that penetration of roads into primary forest facilitates hunting by humans.

Notes and Comments.— During the day Samoan flying foxes will soar on thermal currents with fully extended wings (Cox, 1983). Diurnal activity increases the risk of hyperthermia in these bats at times when daily temperatures and solar radiation are greatest, and mid-day activity may be lower than at dusk and dawn (Thomson et al., 1998; Banack and Grant, 2003). However, soaring can also reduce the energetic costs of flight and under favorable ambient conditions can instead decrease the risk of hyperthermia (Thomson et al., 2002). Samoan flying foxes have wing morphology and flight mechanics more conducive to soaring flight than does the sympatric Pacific flying fox (Norberg et al., 2000).

Males and females seem to form pair bonds (Cox, 1983; Pierson and Rainey, 1992; Banack and Grant, 2003). These bats will scent-mark branches with their chins and sebaceous glands on the back of the neck (Brooke, 2001; Banack and Grant, 2003). Aggressive patrolling and aerial chases between bats seem to be involved with defense of temporary foraging areas; aggressive encounters between bats at feeding sites involve biting, striking with closed wings, and wing clapping (Brooke, 2001; Banack and Grant, 2003).

Stenoderma rufum — Red fruit bat (Family Phyllostomidae)

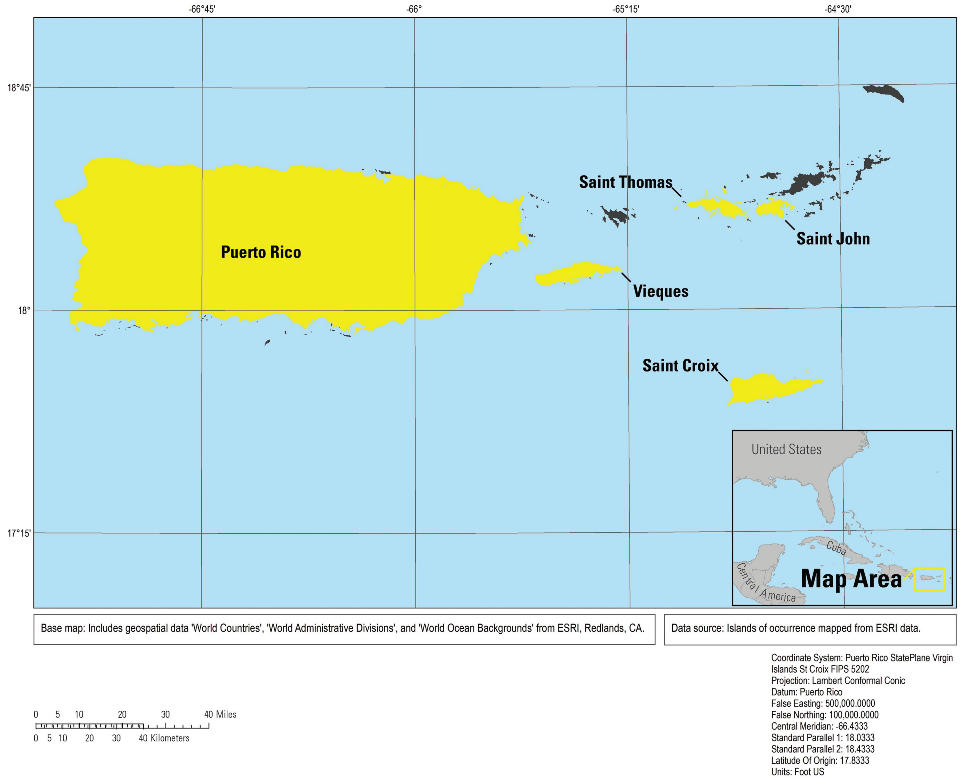
Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. International Union for the Conservation of Nature (2017): Near Threatened.

Territorial Designations.— Puerto Rico Department of Natural and Environmental Resources (2015): Species of Greatest Conservation Need (Vulnerable). U.S. Virgin Islands (Platenberg et al., 2005): Species of Greatest Conservation Need.

Figure 3. Red fruit bat, *Stenoderma rufum* (photo by Michael Gannon, courtesy of the American Society of Mammalogists Mammal Images Library).

Description.— The red fruit bat has a simple nose-leaf, red-tinted tan to dark brown pelage, a small white spot near the shoulder at the junction of each wing with the body, and a small white crescent at the anterior base of each ear (Fig. 3; Genoways and Baker, 1972). Ventral hairs are tipped with gray, and males have scent glands under the white shoulder patches (Gannon et al., 2005). Forearm lengths range 46 to 51 millimeters and body mass 20–31 grams; females average slightly larger than males on Puerto Rico (Jones et al., 1971; Gannon, 1991; Gannon et al., 2005).

Distribution and Systematics.— This species is known from Puerto Rico (including Vieques Island), and from the three islands of St. John, St. Thomas, and St. Croix of the U.S. Virgin Islands where it is considered rare (Fig. 4; Gannon et al., 2005; Kwiecinski and Coles, 2007). This is the only species within the genus *Stenoderma*. Two living subspecies are recognized:



Base map: Includes geospatial data 'World Countries', 'World Administrative Divisions', and 'World Ocean Backgrounds' from ESRI, Redlands, CA.

Data source: Islands of occurrence mapped from ESRI data.

Coordinate System: Puerto Rico StatePlane Virgin Islands St Croix FIPS 5202
Projection: Lambert Conformal Conic
Datum: Puerto Rico
False Easting: 500,000.0000
False Northing: 100,000.0000
Central Meridian: -66.4333
Standard Parallel 1: 18.0333
Standard Parallel 2: 18.4333
Latitude Of Origin: 17.8333
Units: Foot US

FIGURE 4. Approximate distribution of the red fruit bat, *Stenoderma rufum*. Islands where the species occurs are colored yellow.

S. rufum darioi of Puerto Rico (Hall and Tamsitt, 1968), and *S. rufum rufum* of St. John and St. Thomas (Genoways and Baker, 1972).

The taxonomic history of the red fruit bat has been described by Anthony (1918), Hall and Bee (1960), and Gannon et al. (2005). This species was first described in 1813 from a single specimen in the Paris Museum; the locality from which the specimen was collected was unknown, but incorrectly speculated to be Egypt. In the early 1900s, the species was re-discovered based on relatively recent fossil remains from caves in Puerto Rico by Anthony (1918) who pointed out that the original description was based on a specimen in the flesh. However, the red fruit bat was thought to be extinct until living specimens were verified in 1957 (Hall and Bee, 1960; Gannon et al., 1992, 2005). Genoways and Baker (1972) provided a complete taxonomic synonymy of past scientific names applied to the red fruit bat. The generic name *Stenoderma* stems from two Greek words meaning "narrow" and "skin", and the specific epithet is from the Latin word meaning "red". Other English common names include red fig-eating bat (preferred by species experts) and Desmarest's fig-eating bat; a Spanish common name is murciélago frutero native.

HABITATS.— On Puerto Rico, the red fruit bat is best known from tropical rain forest of the Luquillo Mountains of the El Yunque National Forest, but on St. John records are for drier, mixed habitats. Of the three major life zones in the Luquillo Mountains of Puerto Rico, habitat use appears to be limited to the lower elevation tabonuco (*Dacryodes excelsa*) rain forest (Gannon and Willig, 1994). Red fruit bats have been captured at heights up to three meters above paths and streams, and above the forest canopy (as summarized by Genoways and Baker, 1972), as well as at the mouths of canyons opening onto ocean beaches (Hall and Bee, 1960). Areas with gaps in the canopy appear to be selected for movement, foraging, and night roosting (Gannon, 1991). Habitats used by this bat in Puerto Rico are in areas that are currently protected as reserves (El Yunque National Forest) or formerly protected as military reserves (Vieques Island).

FORAGING AND DIETARY ANALYSIS.— Red fruit bats are primarily frugivorous. Wing morphology and attributes of echolocation calls suggest that the red fruit bat is adapted to slow flight in cluttered environments (Norberg and Rayner, 1987; Jennings et al., 2004). The relatively small home ranges (2.1 hectares) do not differ in area between males and females, and individuals show high site fidelity to a single feeding area, at least during the rainy season (Gannon, 1991; Gannon and Willig, 1994). Major dietary items are the fruits of *Cecropia schreberiana, Manilkara bidentata,* and *Prestoea montana* (Gannon and Willig, 1992). It is a major seed disperser for *M. bidentata* (Gannon et al., 2005). Ranges of radio-tagged red fruit bats increased markedly after Hurricane Hugo in 1989, indicating difficulty in obtaining food and suitable roosts (Gannon and Willig, 1994). All information regarding diet, foraging, and habitats is based primarily on studies of the population at the Luquillo Experimental Forest, El Yunque National Forest.

ROOSTING HABITS.— On Puerto Rico these bats are not commonly associated with caves (Rodriguez-Duran, 1998), but instead they roost in foliage in the forest canopy (Gannon and Willig, 1994). Roosting sites are included within foraging ranges, thus minimizing commuting distances (Gannon, 1991). Males and females roost solitarily, and do not form social groups. During the night they spend most of the time roosting in foliage to consume and digest food. Specific diurnal and night roost locations are changed almost daily, and appear to be selected opportunistically (Gannon, 1991).

POPULATION ECOLOGY.— Litter Size, Natality, and Female Reproduction: Litter size is one, based on embryo counts from about seven females (Tamsitt and Valdivieso, 1966; Jones et al., 1971; Genoways and Baker, 1972); reproduction occurs throughout the year on Puerto Rico (Gannon and Willig, 1992). Seven of 12 (58%) females captured in broadleaf tropical forest at the Luquillo Experimental Forest of Puerto Rico during July 1969 were reproductive (Jones et al., 1971; Genoways and Baker, 1972). Reproduction of red fruit bats was negatively impacted by Hurricane Hugo in 1989, with the proportion of juveniles in samples dropping from 30–40% before the hurricane in 1989 to about 17% immediately afterwards and zero in 1991. The proportion of adult females pregnant or lactating declined from at least 55% to less than five percent (Gannon and Willig, 1994). We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as age at first reproduction and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: The most obvious mortality factor affecting red fruit bats is that their populations can be severely impacted by hurricanes (see above). Predation on red fruit bats appears to be very low (Gannon, 1991), but there are no published records of the impacts of predators, disease, or parasites on mortality of this species. Nocturnal activity patterns of red fruit bats are not affected by moon phase, which is consistent with a reduction in visually oriented nocturnal predators on the inhabited islands in comparison with mainland habitats (Gannon and Willig, 1997). It has recently been discovered that red fruit bats have been killed by turbines at wind-power generating facilities in Puerto Rico (Rodríguez-Durán and Feliciano-Robles, 2015).

Population Trend: These bats are rare throughout their very small range. Quantitative statistical evaluations of trends in populations of red fruit bats are unavailable (Ellison et al., 2003). Following the occurrence of Hurricane Hugo in 1989, relative abundance (captures per mist-net hour) in the Luquillo Experimental Forest gradually dropped to about 30% of pre-hurricane levels, and had not recovered three years thereafter (Gannon and Willig, 1994). This impact of the hurricane was more persistent than for two other sympatric frugivorous-nectarivorous species of bats. Causes of the decline were related to an inability to use habitat types other than tabonuco forest, decreased availability of fruit, and increased exposure to climatic factors at roost sites. By 1992 it was feared that the population might have been in danger of disappearing as a result of hurricane-induced habitat alterations (Gannon and Willig, 1994). In 1998, Hurricane Georges also impacted this species, with populations depressed for at least four years afterwards (Gannon et al., 2005).

MANAGEMENT PRACTICES AND CONCERNS.— Loss of this species could have significant impacts on forest tree composition and structure. For the bullet-wood tree in particular (*Manilkara bidentata*), the red fruit bat is likely the most important seed dispersal agent. This bat also may be the most critical seed-disperser of early successional plants immediately after hurricanes (Gannon and Willig, 1994). Gannon et al. (2005) recommend expanding the number and extent of forest reserves in Puerto Rico to provide foraging and roosting habitat for bats. Observations of mortality of red fruit bats and other species of bats at wind power facilities in Puerto Rico cause concern (Rodríguez-Durán and Feliciano-Robles, 2015).

NOTES AND COMMENTS.— Anthony (1918) found fossils of this bat in an inland cave on Puerto Rico, but a living red fruit bat has never been found in a cave on the island.

SPECIES ACCOUNTS: THE UNITED STATES

Choeronycteris mexicana — Mexican long-tongued bat (Family Phyllostomidae)

CONSERVATION STATUS.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2008, 2011a, 2017): Sensitive Species (Arizona, New Mexico state offices). International Union for the Conservation of Nature (2017): Near Threatened. NatureServe (2017): Rounded Global Status G3, Vulnerable.

State Designations: Arizona Game and Fish Department (2012): Tier 1C Species of Greatest Conservation Need; California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern; New Mexico Department of Game and Fish (2006, 2015): Critically Imperiled, Species of Greatest Conservation Need, Sensitive.

DESCRIPTION.— The Mexican long-tongued bat (Fig. 5) has a prominent nose leaf, about five millimeters long, a long rostrum, and a short tail, extending about 10 millimeters beyond the tail membrane (Hoffmeister, 1986; Arroyo-Cabrales et al., 1987).

FIGURE 5. Mexican long-tongued bat, *Choeronycteris mexicana* (photo by J. Scott Altenbach).

The long snout and long tongue with bristle-like tip distinguishes it from *Macrotus californicus*, and the longer snout and presence of the short but conspicuous tail extension distinguishes it from the nearly tailless *Leptonycteris yerbabuenae* and *L. nivalis*, the only other leaf-nosed bats found in the contiguous United States. The pelage color is various shades of brown on the dorsum and lighter on the venter, forearm lengths range 42 to 48 millimeters, and body mass from 10 to 20 grams (up to 25 grams in gravid females) (Hoffmeister, 1986; Arroyo-Cabrales et al., 1987). Campbell (1934:241) noted that "the hind legs are long, and when the bats hang, they resemble nothing so much as plums, hanging by the stems."

Distribution and Systematics.— The distribution of Mexican long-tongued bats within the U.S. is seasonal and generally overlaps the distribution of columnar cacti and agaves (Scott, 2004). They range from extreme southern California, southern Arizona, and southwestern New Mexico (Fig. 6) south to Central America (Arroyo-Cabrales et al., 1987). Rare occurrences have been recorded in southern Texas and southern Nevada (Constantine, 1987; Chapman and Chapman, 1990; Fernandez et al., 2000; Balin, 2009; Ammerman et al., 2012a). Records from southern California also may be extralimital records (Fleming et al., 2003); Mexican long-tongued bats seemed fairly numerous around San Diego in the 1940s, but this was considered a singular migration or dispersal event (Olson, 1947; Huey, 1954a; Barbour and Davis, 1969). However, additional records in California from San Diego County, Los Angeles County, Orange County, and Ventura County occasionally have been recorded in subsequent years through 1995 (Constantine, 1998a). This bat was first reported in Arizona in 1904 based on a specimen from the Chiricahua Mountains (Miller, 1906), but was apparently unknown from New Mexico until 1956 when a specimen was taken in Skeleton Canyon, Peloncillo Mountains, Hidalgo County (Findley, 1957).

This is a New World leaf-nosed bat (Family Phyllostomidae). The species was named by Tschudi in 1844, and there have been no further taxonomic changes (Arroyo-Cabrales et al., 1987). There are no recognized subspecies. The name *Choeronycteris* is derived from two Greek words meaning "pig" and "bat". The specific epithet is based on geography. Other English common names used in the literature include long-tongued bat and hog-nosed bat.

Habitats and Relative Abundance.— Mexican long-tongued bats are migratory, visiting the southwestern United States during warm months and migrating to Mexico in winter (Fleming et al., 2003). In the Peloncillo Mountains of New Mexico, this species is present (but at low abundance) from May to October (for example, Mumford and Zimmerman, 1962; Mumford et al., 1964; Scott, 2004). Similar seasonality has been reported in southern Arizona (for example, Hoffmeister, 1986; Scott, 2004).

Habitat around roosts of Mexican long-tongued bats observed by Cryan and Bogan (2003, see "Roosting Habits" below) in Arizona and New Mexico was Madrean evergreen woodland or semi-desert grassland, with roosts occurring within one kilometer of streams and within 0.5 kilometers of riparian deciduous vegetation, and with agaves (*Agave schotti* or *A. palmeri*) present in the vicinity of roosts. Elevations of these roosts averaged 1,477 meters (range 975–1,846). Hoffmeister and Goodpaster (1954) found them roosting in habitats ranging from the lower edge of the oak zone up through the pine-fir belt in the Huachuca Mountains of Arizona. Hoffmeister (1986) described their habitat as mountains in southeastern Arizona that have trees. In New Mexico, the habitats around roosts in occupied caves were described as piñon-juniper, oak, and manzanita in the hills and sycamore trees in riparian bottoms (Findley et al., 1975).

There have been few published surveys of bats in areas within the distribution of Mexican long-tongued bats that allow assessment of their relative abundance, although limited data suggest relative abundance is low. As examples, two were taken in nets over water in Hidalgo County, New Mexico among 108 bats of 10 species (ranking ninth in relative abundance; Mumford et al., 1964)

Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 6. Approximate distribution of the Mexican long-tongued bat, *Choeronycteris mexicana*. Species range shown in yellow; records in southern Nevada and parts of Texas not depicted (see text, Ammerman et al., 2012a).

and in the Huachuca Mountains in southern Arizona, Mexican long-tongued bats ranked eleventh in relative abundance among 13 species documented (two captures out of 145 individuals; Sidner and Davis, 1994).

Foraging and Dietary Analysis.— Mexican long-tongued bats are nectar and pollen feeders and are well-known pollinators of several species of columnar cacti, agaves, and other plants in the United States, Mexico, and Central America (for example, Hevly, 1979; Valiente-Banuet et al., 1996; Arizaga et al., 2000; Arias-Cóyotl et al., 2006; Trejo-Salazar et al., 2015). In the deserts of southern Arizona and northern Mexico, stomach contents of this species consisted mainly of pollen grains from agave flowers but also included pollen from ceroid cacti (such as giant saguaro, *Carnegiea gigantea*) and a range of other plants (Hevly, 1979). The giant saguaro cactus has open flowers at night when bats are active and requires cross-pollination for fertility (McGregor et al., 1962). Mexican long-tongued bats have been shown experimentally to be effective pollinators of this iconic plant (Alcorn et al., 1961).

In some areas, some species of columnar cacti and agaves are dependent on nocturnal pollination for successful reproduction, and nectar-feeding bats may be their chief pollinators (Valiente-Banuet et al., 1996; Arizaga et al., 2000). However, in the southwestern U.S. these bats are not their exclusive pollinators. Although the absence of lower incisors indicates specialization for nectar feeding (Howell, 1974), Mexican long-tongued bats also eat cactus fruits and may act as seed dispersers (Godínez-Alvarez and Valiente-Banuet, 2000). When feeding on nectar, these bats have been timed to visit individual flowers an average of less than one second per flower (Arizaga et al., 2000), but can hover in flight for up to 17 seconds (Voigt and Winter, 1999).

Roosting Habits.— Roosts of Mexican long-tongued bats can be in shallow caves, rock shelters and wide rock crevices, abandoned mines, tunnels, and buildings (Campbell, 1934; Olson, 1947; Huey, 1954a; Baker, 1956a, Mumford et al., 1964; Cryan and Bogan, 2003). Roosting places are often in light shade rather than dark recesses (Findley et al., 1975). Hoffmeister and Goodpaster (1954) reported these bats to be present in nearly every mine tunnel or cave they visited in the Huachuca Mountains of southeastern Arizona in 1949–1951, often roosting at the same sites as Townsend's big-eared bats. This observation of co-occurrence of the two species was also made in the Huachuca Mountains in 1933 (Campbell, 1934).

Mexican long-tongued bats seldom roost in tight clusters but can form colonies in the U.S. that are small (less than 50 and usually fewer than 17; Hoffmeister and Goodpaster, 1954; Huey, 1954a; Cockrum and Ordway, 1959; Cryan and Bogan, 2003; Fleming et al., 2003). Average group size was 4.5 bats at 18 roost sites visited in Arizona and New Mexico in 1999, where bats roosted in well-lit areas near entrances (Cryan and Bogan, 2003). Roosting bats are usually alert and quick to exit roosts upon even minor disturbance (Cockrum and Ordway, 1959; Mumford and Zimmerman, 1962; Mumford et al., 1964). Year-to-year fidelity to the same roosting sites or sites within the immediate proximity has been documented (Mumford et al., 1964; Cryan and Bogan, 2003).

The first record of Mexican long-tongued bats in southern California was of a group of five individuals roosting on rafters in a dark corner of a garage in San Diego in 1946; later that year a few others were noted roosting in basements and garages in the same region (Olson, 1947). Subsequent investigations found these bats roosting at 11 other locations (where 39 bats were collected) in the San Diego area, all in or around buildings and in light shade (Huey, 1954a). They also are known to roost during the day in buildings in Arizona and New Mexico (Hoffmeister and Goodpaster, 1954; Cryan and Bogan, 2003). This species also will night-roost in abandoned buildings (Findley, 1957; Watkins et al., 1972).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Females give birth and raise young while in the southwestern United States during summer. Four of five bats observed roosting in a small cave in the Peloncillo Mountains of New Mexico each had a single young in June of 1962 (the fifth was apparently non-reproductive; Mumford et al., 1964) and six observed in June 1960 each had a single young or fetus (Mumford and Zimmerman, 1962); one female with a single young was also reported from New Mexico by Findley et al. (1975). Campbell (1934) and Hoffmeister (1959) each also reported single cases of an adult female with one young attached in southern Arizona during July and August. Four females taken from Colossal Cave in southern Arizona during May 1960 each had single young (Alcorn et al., 1961). Single embryos were reported from one female taken in Coahuila, one taken in Jalisco, and one taken in Sinaloa, Mexico (Baker, 1956a; Jones et al., 1972; Watkins et al., 1972). Thirty-five female Mexican long-tongued bats taken in southern Arizona during August in 1949–1951 had no embryos (Hoffmeister and Goodpaster, 1954). We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as age at first reproduction and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: We are unaware of published literature with information on mortality factors affecting this species.

Population Trend: Mexican long-tongued bats are the least common of the three species of nectar feeding bats (*Leptonycteris nivalis* and *L. yerbabuenae* are the other two species) that can be found seasonally in parts of the southwestern United States, where adult females and young are regularly found to outnumber males (Hoffmeister and Goodpaster, 1954; Fleming et al., 2003). The three largest colony sizes observed in Arizona and New Mexico during 1999 were 17, 14, and 11 bats (Cryan and Bogan, 2003), a colony of 40–50 was observed in a building in southern California in 1946 (Huey, 1954a), and a count of 176 was reported at an unspecified U.S. location in a compilation by Ellison et al. (2003).

Cryan and Bogan (2003) compiled a list of 39 historically known locations of roosts of long-tongued bats in Arizona and New Mexico. They visited 24 of these sites in summer 1999 and reported the bats present at 18 of the 24 locations (75%). Young of the year were observed at a minimum of 71% of the sites, suggesting successful reproduction in the summer range. Regarding population status, Cryan and Bogan (2003:316) remarked: "Considering the number of individuals we encountered and the relatively high rate of recurrence at historical sites, we do not have sufficient evidence to conclude that *C. mexicana* populations have increased or decreased in recent years."

MANAGEMENT PRACTICES AND CONCERNS.— Given the habitats associated with roosting locations and the variety and types of roosts occupied, it is likely that loss of riparian habitat is a greater threat to this species in the southwestern U.S. than is loss of roosts (Cryan and Bogan, 2003). Very little information has been well-documented for this species within the U.S. concerning its population ecology, foraging habitat, and interactions with food plants.

NOTES AND COMMENTS.— Olson (1947) was bitten on the hands multiple times while capturing these bats between 18 and 28 September 1946. On 30 September he developed cellulitis and lymphangitis in one arm, which responded to antibiotics during four days of treatment. However, three days afterwards he had to be hospitalized for four days with severe headaches, nausea, and fever, which were treated with penicillin, morphine, ice packs, and intravenous glucose and saline. He could not account for any other source for this illness other than the bat bites (Olson, 1947).

Corynorhinus rafinesquii — Rafinesque's big-eared bat (Family Vespertilionidae)

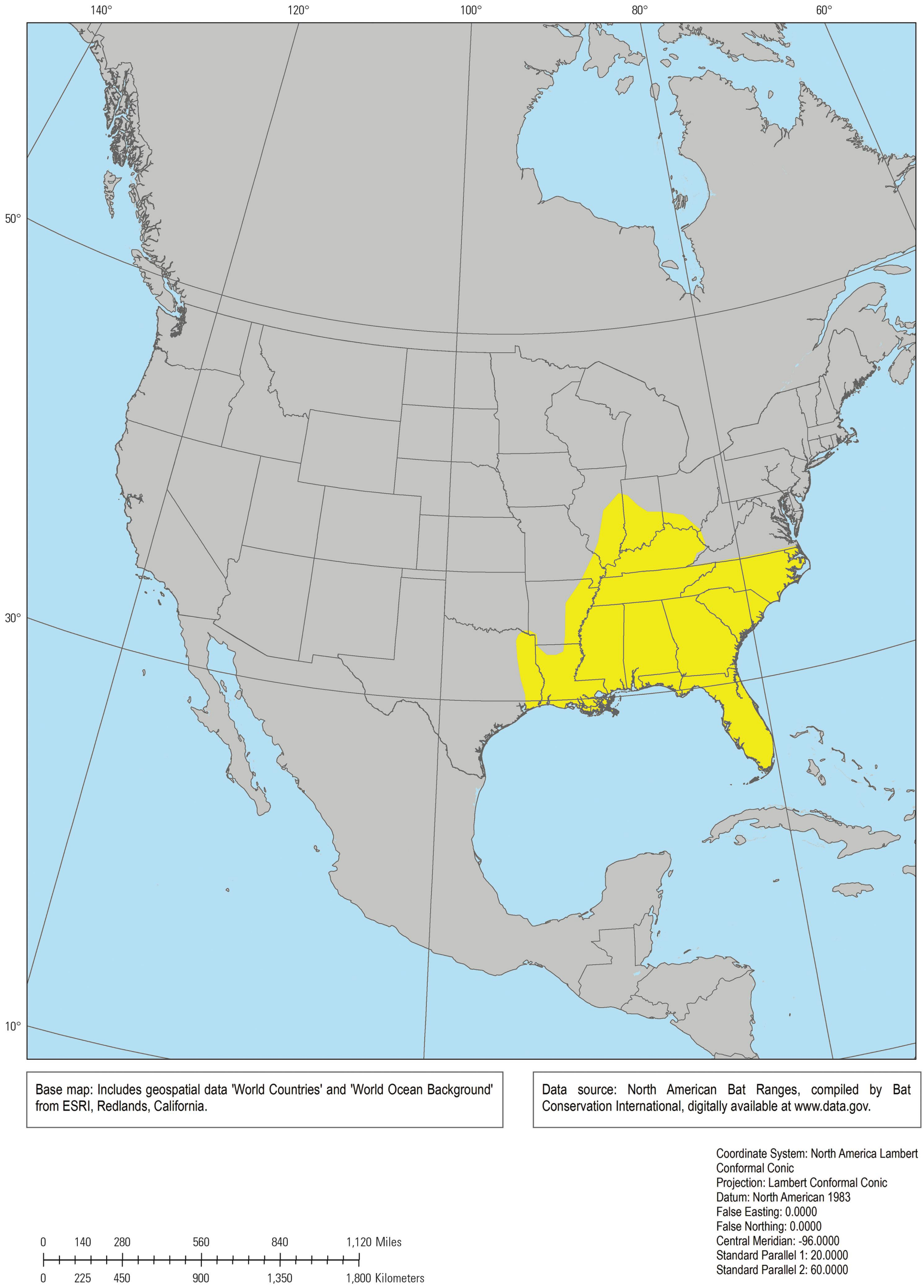
CONSERVATION STATUS.— **National and International Designations:** U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G3, Vulnerable.

State Designations: Alabama Department of Conservation and Natural Resources (2005, 2015a,b): Priority 1 Species of Greatest Conservation Need, Highest Conservation Concern. Arkansas Game and Fish Commission (Fowler, 2015): Species of Greatest Conservation Need. Florida Fish and Wildlife Conservation Commission (2012): Species of Greatest Conservation Need. Georgia Department of Natural Resources (2015, 2016): Rare, High Priority. Illinois Department of Natural Resources (2015): State Endangered. Indiana Department of Natural Resources (2006, 2015): Special Concern, Species of Greatest Conservation Need. Kentucky Department of Fish and Wildlife Resources (2013): Species of Greatest Conservation Need. Louisiana Department of Wildlife and Fisheries (2015): Tier III Species of Greatest Conservation Need. Maryland Department of Natural Resources (2005): Species of Greatest Conservation Need (not included in Maryland Department of Natural Resources 2016). Mississippi Department of Wildlife, Fisheries and Parks (2005, 2015): Species of Greatest Conservation Need. Missouri Department of Conservation (2016): Species of Conservation Concern, Critically Imperiled. North Carolina Wildlife Resources Commission (2014): Threatened. Ohio Department of Natural Resources Division of Wildlife (2015): Species of Concern. Oklahoma Department of Wildlife Conservation (2005, 2016): Species of Greatest Conservation Need Tier II. South Carolina Department of Natural Resources (2005, 2015) State Endangered, Highest Priority Species of Greatest Conservation Need. Tennessee Wildlife Resources Agency (2005, 2015): Tier I Species of Greatest Conservation Need. Texas Parks and Wildlife (2015): State Threatened. Virginia Department of Game and Inland Fisheries (2005, 2015a, b): Tier I Species of Greatest Conservation Need, State Endangered. West Virginia Division of Natural Resources (2015): Priority 1 Species of Greatest Conservation Need.

Description.— Extremely large ears distinguish Rafinesque's big-eared bat (Fig. 7) from all others in its range except eastern subspecies of Townsend's big-eared bat. Unlike Townsend's big-eared bat, the hairs on the feet extend beyond the toes and the ventral pelage is bicolored with dark, blackish bases and light tips (Sealander and Heidt, 1990; Schmidly, 1991). Body mass ranges 7.9 to 9.5 grams in males and 7.9 to 13.6 grams in females, and forearm lengths range 39–46 millimeters (Jones, 1977; Clark, 1990; Schmidly, 1991). A large gland is present on both sides of the snout between the eyes and nostrils.

Figure 7. Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (photo by J. Scott Altenbach).

Distribution and Systematics.— Rafinesque's big-eared bat occurs in the southeastern United States, including Florida north and westward to southern and western Virginia, southern West Virginia, southern Ohio, southern Indiana, southern Illinois, southern Missouri, eastern Oklahoma, and eastern Texas (Fig. 8). A state-by-state review of surveys for the presence of this species was provided by Clark (2003), with a detailed update by Bayless et al. (2011). Genetic analysis



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 8. Approximate distribution of Rafinesque's big-eared bat, *Corynorhinus rafinesquii*. Species range shown in yellow, but extends into southwestern Virginia (see text).

indicates that *C. rafinesquii* is the older, most basal of the living species of *Corynorhinus* (Piaggio and Perkins, 2005; Lack and Van Den Bussche, 2009). Two subspecies were recognized by Handley (1959) based on morphology: *C. rafinesquii rafinesquii* distributed primarily in the inland states, and *C. rafinesquii macrotis* found within the Gulf and Atlantic coastal states (Jones, 1977). However, modern phylogenetic analysis fails to distinguish these two subspecies, but instead documents two overlapping clades that do not follow the earlier proposed subspecies distributions (Piaggio and Perkins, 2005; Piaggio et al., 2011).

Earlier literature may refer to this species as *C. macrotis*. For explanation of recent changes in nomenclature of this and other bats formerly grouped under the genus *Plecotus*, see the species account in this volume for *Corynorhinus townsendii*. Jones (1977) provides a taxonomic synonymy of past scientific names applied to Rafinesque's big-eared bat prior to the more recent changes noted in our account for Townsend's big-eared bat. The generic name *Corynorhinus* stems from Greek words meaning "club" and "nose". This bat is named in honor of C.S. Rafinesque, a French naturalist and explorer of the United States during the early 1800's. Other English common names include eastern big-eared bat, southeastern big-eared bat, eastern lump-nosed bat, eastern mule-eared bat, and eastern long-eared bat.

Habitats and Relative Abundance.— Rafinesque's big-eared bat is typically found in forested regions of the southeastern U.S., especially in bottomland hardwood forests (which have declined markedly since colonization times, for example, Twedt and Loesch, 1999). Local distributions are sometimes poorly known (Jones, 1977; Clark, 2003; Martin et al., 2011), but they also utilize upland hardwood and pine forests in some areas, particularly mountainous regions with caves and mines in the northern portions of their range (Lacki and Dodd, 2011; Loeb, 2017). In contrast to generally high relative abundance in bottomland hardwoods, bat community surveys in pine forests typically yield relative abundances of two percent or fewer of total captures or acoustic detections of all bat species that can be identified as Rafinesque's big-eared bats (reviewed by Debelica-Lee and Wilkins, 2014; Morris et al., 2010). Findings on habitats and relative abundance of these bats are given below on a state-by-state basis.

Arkansas: Rafinesque's big-eared bats were the second most abundant species of bat encountered in mist-netting surveys in bottomland hardwood forests of six wildlife management areas and national wildlife refuges in Arkansas (65 out of 302 bats of eight species; Medlin and Risch, 2008). They also ranked second in abundance (71 captures among 556 bats of eight species) at 35 sites surveyed during summers 1997–1999 in bottomland hardwood forest of the Rex Hancock/Black Swamp Wildlife Management Area of eastern Arkansas (Hoffman, 1999).

Georgia and South Carolina: In Georgia, these bats were thought to occur throughout the state, but with an absence of records from the Piedmont and upper Coastal Plain thought to be due to low survey effort; they ranked low in relative abundance (26 records) among 1,222 combined museum and capture records of bats of 16 species (Menzel et al., 2000). Menzel et al. (2003) examined records of all species of bats across the four physiographic provinces of South Carolina based on 1,002 museum specimens and reports of 2,002 bats captured during surveys. Rafinesque's big-eared bat was found in three of the provinces (Blue Ridge Mountains, Upper and Lower Coastal Plains) but no records were found for the Piedmont. Reasons for lack of Rafinesque's big-eared bats in the Piedmont remain unknown. This species was intermediate in relative abundance of records (264) among 3,004 combined museum and capture records of bats of 14 species compiled for the state.

Louisiana and Mississippi: This species was the most abundant bat in mist-net surveys of bottomland hardwood forests in northeastern Louisiana (56 bats among 112 bats of four species; Rice, 2009). Areas in west-central Louisiana around concrete bridges used as day roosts by this species consisted of greater proportions of deciduous forest than areas around bridges not used as roosts (Lance et al., 2001). They ranked fifth in relative abundance (29 Rafinesque's big-eared bats captured among 419 bats of seven species) in extensive mist-net surveys conducted on 113 nights at 79 sites in nine study areas across Mississippi during 2002–2006, and were captured at two study areas in habitats characterized as bottomland hardwood forests, mixed hardwood forests, upland mixed hardwood forests, and swamp forest (McCartney, 2007). A second mist-netting survey in summer 2007 focused on four refuges within the Theodore Roosevelt National Wildlife Refuge complex in western central Mississippi (McCartney and McCartney, 2008). No Rafinesque's big-eared bats were captured in 28 nights of netting at 23 sites, despite documentation of 201 bats of five other species (McCartney and McCartney, 2008). In Mississippi, upland pine forest with abandoned buildings has provided habitat for maternity colonies (Martin et al., 2011).

North Carolina: In the Coastal Plain of North Carolina, this species tends to roost in trees and is associated with river swamps and bay lakes bordered by mature swamp forests (Clark et al., 1985; Loeb, 2017). Rafinesque's big-eared bats are unlikely to undergo extensive migrations, and in eastern North Carolina can be found in the same areas during winter and summer (Clark, 1990). Colonies in abandoned buildings in eastern North Carolina (a region without caves) were in areas with more closed-canopy forest than were colonies in unused abandoned buildings, and all were within one kilometer of a major water body (Clark, 1990). Rafinesque's big-eared bats ranked sixth in relative abundance (20 captured out of 452 individuals of eight species) of bats netted around water and at corridors on the coastal Plain of North Carolina during summer (forest types unspecified), but were seldom detected by acoustic monitoring (Grider et al., 2016).

FORAGING AND DIETARY ANALYSIS.— This species reportedly emerges only after dark and does not forage in twilight (Jones, 1977; Sealander and Heidt, 1990). Wing morphology and flight characteristics suggest that these bats are slow flyers with excellent maneuverability, and perhaps an ability to hover and glean at times (Lacki and Ladeur, 2001), characteristics that are adaptive in complex forest habitats but that may make them less competitive with more common, faster-flying bats in open areas (Belwood, 1992). In northeastern Arkansas, these bats were more likely to be captured over land rather than over water, and were associated with more dense vegetation cover that may provide higher insect prey abundance (Medlin and Risch, 2008).

Foraging areas of these bats averaged across studies ranged 93 to 165 hectares, with maximum flight distances from roosts ranging up to 1.2 km (Lacki and Dodd, 2011). Foraging areas of five Rafinesque's big-eared bats tracked by radio telemetry in southeastern Kentucky overlapped, were from 62–225 hectares in area, and were at locally higher elevations (Hurst and Lacki, 1999). Centers of foraging areas ranged from about 0.1 to 1.2 kilometers away from the diurnal roost. The bats foraged primarily in oak-hickory forest rather than yellow poplar or beech-maple forests, but oak and oak-hickory forests were also closer to the roosts (Hurst and Lacki, 1999). Four male Rafinesque's big-eared bats radio tracked in South Carolina during the late summer and early autumn did most of their foraging during the first four hours after sunset and two hours before sunrise (Menzel et al., 2001). These bats foraged in young pine stands in upland areas rather than bottomland habitats (only 9% of locations) and exhibited relatively small home ranges (about 93 hectares using the 95% adaptive kernel method). In southwestern Kentucky, 39 radio-tracked Rafinesque's big-eared bats of both sexes foraged over individual home ranges averaging 170 ± 21 (SE) hectares, but with the 5 adult male home ranges averaging 96 ± 52 hectares (Johnson and Lacki, 2013a). There the bats fed primarily on moths, and home ranges of foraging females were associated with both wetland habitat and upland deciduous forest but not open fields; foraging activities followed the simultaneously monitored distribution and availability of moths, which constituted 80% of prey (Johnson and Lacki, 2013a).

Examination of fecal pellets and culled insect wings from beneath roosts of Rafinesque's big-eared bats in Kentucky suggests that these bats are moth specialists, preying on moths with wingspans from 31 to 57 millimeters: the diet is greater than 80% moths followed by beetles and other groups as the next most utilized dietary components (Hurst and Lacki, 1997; Lacki and Ladeur, 2001). This generally holds true across study areas (Lacki and Dodd, 2011). Moths that were consumed in the Kentucky studies were predominantly sphinx moths and noctuids of the genus *Catocala*, many members of which feed on oaks and hickories as larvae (Hurst and Lacki, 1997, 1999). Further analysis of fecal pellets sampled in Kentucky using DNA-based prey identification techniques showed that prey size may be over-estimated using earlier methods, but verified that lepidopterans (particularly macrolepidopterans) were the primary prey (Dodd et al., 2015).

In addition to a diet rich in moths, dietary analysis of fecal pellets from a North Carolina colony revealed that although 67% of the sample volume were lepidopterans, 31% were tabanid dipterans (for example, horse flies), suggesting that these bats could contribute to control of tabanids as pests and vectors of disease (Ellis, 1993). Analysis of fecal pellets from the more southern parts of their distribution in Florida and Louisiana also confirmed that Rafinesque's big-eared bats primarily eat lepidopterans, and that they will feed year-round (Whitaker et al., 2007; Gregory et al., 2014). In a review of several feeding studies, Lacki and Dodd (2011) reported that moths most frequently taken in order of presence in the diet belong to the families Noctuidae, Geometridae, Sphingidae, and Arctiidae.

ROOSTING HABITS.— Rafinesque's big-eared bats have been reported to roost in hollow trees, under loose tree bark, in caves, and in a variety of human-made structures including culverts, bridges, abandoned buildings, wells, cisterns, barns, empty oil storage tanks, abandoned house trailers, and mines (Moore, 1949; Pearson, 1962; Mumford and Whitaker, 1982; Schmidly, 1991; Hurst and Lacki, 1999; Lance et al., 2001; McDonnell, 2001; Clark, 2003; Felts and Webster, 2003; Gooding and Langford, 2004; Trousdale and Beckett 2004, 2005; McCartney, 2007; Martin et al., 2011; Sasse et al., 2011; Trousdale, 2011; Clement and Castleberry 2013b,c). Rafinesque's big-eared bats are often found roosting at the same sites with tricolored bats (*Perimyotis subflavus*) and southeastern myotis (*Myotis austroriparius*), and to a lesser degree will also share roosts with other species (for examples, Jones and Suttkus, 1975; Jones, 1977; Mumford and Whitaker, 1982; Clark, 1990; Hurst and Lacki, 1999; Ferrara and Leberg, 2005b).

Winter Roosts in Caves and Human-Made Structures: Winter roosts of Rafinesque's big-eared bats include caves, cavities in rock piles (talus caves), mines, cisterns, buildings, and hollow trees. Rafinesque's big-eared bats consistently occupy hibernacula throughout the winter in the northern parts of the range, but may move between colonies in late winter and early spring (Hoffmeister and Goodpaster, 1962). In large areas of their range, these bats may not undergo prolonged, deep hibernation during winter.

In geologically suitable areas, Rafinesque's big-eared bats regularly winter in caves and mines. According to Sealander and Heidt (1990), in the northern part of its range, this species hibernates in the cool twilight zone of caves, often within 10–35 meters of entrances. One sandstone cave monitored in southeastern Kentucky from 1993–1998 was used by this species throughout the year and housed from 14 to 49 bats in winter (Hurst and Lacki, 1999). This species hibernates in silica mines and caves during winter in southern Illinois (Hoffmeister, 1989). Solitary hibernators were reported in a cave and a talus cave or rock shelter in Arkansas (Saugey et al., 1993). Hibernating individuals at Mammoth Cave National Park in Kentucky aroused from their relatively shallow (compared to other North American hibernating bats) winter torpor (skin temperature 13.9 degrees Celsius [ºC] ± 0.6 SE) near sunset every 2.4 days, and switched winter roosts in caves (and abandoned buildings) every 4.1 days (549 to 5,964 meters between consecutive roosts), presumably foraging after some arousals (Johnson et al., 2012b).

Counts of hibernating Rafinesque's big-eared bats at 10 hibernacula in caves, abandoned mines, and rock shelters in the Appalachian Mountains and Central Plateaus of Kentucky, North Carolina, and Tennessee totaled 4,100 bats, ranging from about 600 to 1,345 bats per site (Bayless et al., 2011). The largest local population reported is about 1,700 bats, which utilized a group of abandoned mines in both winter and summer in the North Carolina part of Great Smoky Mountains National Park (Currie, 2000a). In southern parts of the distribution, they are found torpid less frequently in winter (Jones and Suttkus, 1975). An abandoned mobile home in central Florida housed a colony of this species year-round, but colony size was generally larger in winter (about 60 maximum) than early summer (31 maximum; Clark, 2003).

These bats often spend winter in other human-made structures. In southwestern Arkansas, use of roosts in 37 water wells was studied during winter months (October-March) over a 21-year period (Sasse et al., 2011). Most counts were of 20 or fewer bats per well, with the largest numbers (40 or more) counted in December-February and a maximum of 103 at one well in February 2006 (Sasse et al., 2011). These relatively permanent structures appear to have allowed some persistence of the species despite loss of regional bottomland hardwoods and associated roosts, although counts suggest a possible declining trend (Sasse et al., 2011). Rafinesque's big-eared bats were reported hibernating in three small clusters of about 20 bats each in an open eight-meter deep cistern in Tennessee in 1950 (Hoffmeister and Goodpaster, 1962), a roost which had been occupied annually for many years previously and continued to be occupied through 1962, further suggesting that these bats may exhibit site fidelity to wells and cisterns at suitable locations. Bridges and buildings were used as winter roosts in Louisiana but to a lesser extent than in summer (Jones and Suttkus, 1975; Ferrara and Leberg, 2005b). Only solitary bats were observed under concrete bridges during the colder months in the De Soto National Forest in Mississippi, whereas from one to 25 Rafinesque's big-eared bats (averaging four to five) were found using them during the maternity season (Trousdale and Beckett, 2004). Limited searches elsewhere in Mississippi found no Rafinesque's big-eared bats roosting in 22 caves and 10 cisterns, but two solitary bats and one group of 5 were found roosting in three culverts during winter (McCartney, 2007).

Winter Roosts in Hollow Trees: In areas without many caves and mines, Rafinesque's big-eared bats winter in trees. Large, old hollow trees are used as winter roosts in Mississippi (Martin et al., 2011; Fleming et al., 2013a). In eastern Mississippi, trees with cavities used by Rafinesque's big-eared bats in winter had larger girths and larger cavity volumes than trees with cavities that were unoccupied, but in spring trees that were selected were similar in girth and cavity size (Fleming et al., 2013a). On the landscape scale, roost trees found in winter during the Mississippi study were at lower elevations than unoccupied trees with cavities (Fleming et al., 2013a). Radio-tagged individuals roosting in hollow trees in two lakes in central Georgia during winter switched roosts on average every 6.9 days (range one to 22) and moved three to 210 meters between successive roosts (Clement and Castleberry, 2013b). Roost trees used during winter in the Georgia study were less likely to have low openings and were more likely to be in water tupelo trees than were unoccupied trees; traits of trees used as winter roosts were similar to those of trees used in summer, but those used in winter tended to lack elevated openings, had a narrower range of sizes, were more chimney-like, and had rougher interior surfaces (Clement and Castleberry, 2013b).

Six male and six female bats were radio tracked for periods of one to 20 days in autumn and early winter to determine roosting habits at Upper Ouachita National Wildlife Refuge in northeastern Louisiana (Rice, 2009). Males were tracked to an average of 2.2 roosts, spending 4.4 days per tree (up to 11 days), and traveling an average of 177 meters between roosts, whereas females used an average of 1.7 roosts and spent 2.8 days per roost (up to six days), traveling an average of 291 meters between roosts (up to 1,726 meters). As in the Georgia study, an important finding in

Louisiana was that roosts used by wintering Rafinesque's big-eared bats were mainly hollow water tupelo trees with chimney-like openings and no basal openings (Rice, 2009).

Warm Season Roosts in Caves and Mines: One sandstone cave monitored in southeastern Kentucky from 1993–1998 housed up to 118 Rafinesque's big-eared bats in summer (Hurst and Lacki, 1999). The cave was also used in winter, but areas of the cave used by the maternity group in summer were consistently warmer than chambers used for hibernation. Radio-tagged bats monitored at this cave showed high roost fidelity in summer (Hurst and Lacki, 1999). A gated mine in northwestern South Carolina was known to house a maternity colony of 40–60 bats each year for at least 12 years (Loeb and Britzke, 2010). Abandoned mines are used as roosts by this species during summer in the North Carolina portion of Great Smoky Mountains National Park (Currie, 2000a).

Warm Season Roosts in Hollow Trees: During summer Rafinesque's big-eared bats exploit a diverse array of trees as roosts. Many species of large-diameter hollow trees have been documented as day or night roosts for Rafinesque's big-eared bats, especially in forested wetlands. The rates at which cavities occur in trees of bottomland hardwood forests can vary with species and size of trees (Stevenson, 2008). Use of specific individual trees can span multiple years (Loeb and Zarnoch, 2011). Species of trees used as roosts include black gum (*Nyssa sylvatica*), water tupelo (*Nyssa aquatica*), bald cypress (*Taxodium distichum*), eastern cottonwood (*Populus deltoides*), southern magnolia (*Magnolia grandiflora*), American beech (*Fagus grandifolia*), American sycamore (*Platanus occidentalis*), shellbark hickory (*Carya laciniosa*), pignut hickory (*Carya glabra*), sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), river birch (*Betula nigra*), yellow poplar (*Liriodendron tulipifera*), and oaks (*Quercus* spp.; Clark, 1990, 2003; Hoffman, 1999; Lance et al., 2001; Gooding and Langford, 2004, Mirowsky et al., 2004; Trousdale and Beckett, 2005; Carver and Ashley, 2008; Stevenson 2008; Loeb and Zarnoch, 2011; Martin et al., 2011; Clement and Castleberry, 2013b,c; Fleming et al., 2013a; Stuemke et al., 2014). In many areas, Rafinesque's big-eared bats roosting in hollow trees in bottomland hardwood forests switch roosts often, but they may be loyal to clusters of trees in a relatively small area (Clark, 2003; Gooding and Langford, 2004; Rice, 2009). Below we summarize findings regarding roosts in hollow trees by state.

***Arkansas and Tennessee*:** Three radio-tagged Rafinesque's big-eared bats captured in bottomland hardwood forest of the Rex Hancock/Black Swamp Wildlife Management Area of eastern Arkansas roosted in four hollow water tupelo trees with high openings (Hoffman, 1999). In western Tennessee, six Rafinesque's big-eared bats radio tracked to roosts in Pinson Mounds State Archaeological Park used living, hollow water tupelo trees as roosts, and favored hollow trees larger in girth than trees that were unused, and larger than hollow trees used by sympatric southeastern myotis (Carver and Ashley, 2008).

***Georgia*:** Primarily using radio telemetry and transect surveys that searched 1,731 hollow trees in a floodplain study area in central Georgia, Clement and Castleberry (2013c) found Rafinesque's big-eared bats roosting in 170 hollow trees and counted a total of 870 bats at these roosts (730 bats were in 30 maternity colonies, which were in trees with larger internal cavities). Nearly all roost trees were in semi-permanently flooded or seasonally flooded areas. Occupied trees were larger and had larger cavity volumes and smoother interior walls than unoccupied trees, suggesting that avoidance of predators (snakes are more apt to climb rougher internal walls in summer) is an important aspect of summer roost selection (Clement and Castleberry, 2013c).

***Kentucky*:** Rafinesque's big-eared bats radio tracked in summer on the floodplain of the Ohio River in Kentucky (Johnson et al., 2012a) switched roosts every three days regardless of sex or reproductive status; distances moved between consecutive roosts averaged 829 meters, with males and lactating females moving the shortest distances. Counts of emerging bats in the Kentucky study ranged from one to 96 (mean 18.3) bats at female roosts, and one to 13 (mean 2.9) at male roosts (Johnson et al., 2012a). In southwestern Kentucky, 59 of 64 diurnal roosts found in summer (through radio tracking of 49 bats captured while foraging) were in hollow trees in low-lying wetlands (Johnson and Lacki, 2013a). Bats in Kentucky used torpor in the summer, with the degree of torpor in females varying by stage of reproduction (Johnson and Lacki, 2013b,c). Network analysis of the radio-tracked bats in Kentucky (Johnson et al., 2012a) provided details of their fission-fusion social structure, a social system that appears to be common among species of bats that form colonies in trees in North America (for example, Kurta, 2005; Patriquin et al., 2010; Willis and Brigham, 2004).

***Louisiana*:** At D'Arbonne National Wildlife Refuge 44 known roost trees were all in cavities of hollow water tupelo trees with triangular basal openings (Gooding and Langford, 2004). Numbers of bats using these trees varied greatly from day to day, with one to 80 bats observed when present; one radio-tagged female moved among at least four roost trees during a 14-day period (Gooding and Langford, 2004). In bottomland hardwood forests at Upper Ouachita National Wildlife Refuge in northeastern Louisiana, group size ranged from solitary individuals to colonies of up to 150, with day-to-day variability in colony sizes (Rice, 2009). Repeated searches of 57 hollow trees along a stretch of the Ouachita River, conducted mostly in warm months, found that 32 water tupelo (the most predominant trees) and two bald cypress were used by Rafinesque's big-eared bats. Much variability occurred among roost trees in their frequency of use, with bats found most often in trees with higher internal cavities (Rice, 2009).

***Mississippi*:** Radio-tracking studies in southeastern Mississippi revealed that Rafinesque's big-eared bats favored roost trees of the genus *Nyssa* (Trousdale and Beckett, 2005). All the roosts in trees found in the southeastern Mississippi study were in bottomland hardwood habitat. Openings to cavities used as roosts averaged 5.2 meters in height, and trees averaged 18.5 meters in height with an average diameter at breast height of 79 centimeters; canopy closure was high (greater than 90%) at roost trees and surrounding 0.1–hectare plots (Trousdale and Beckett, 2005).

***South Carolina*:** In the largest old growth bottomland hardwood forest remaining in the U.S., 43 roosts of Rafinesque's big-eared bats were located by visual searches and radio tracking of 15 individuals (Lucas et al., 2015). In this study, conducted in the Congaree National Forest on the South Carolina Coastal Plain, bats roosted in large-diameter hollow trees in areas with high densities of hollow trees, with most using live-damaged trees in semi-permanently flooded and seasonally flooded habitat (Lucas et al., 2015). Females in maternity colonies (ranging in size from about 6 to 100 bats, average ca. 40) switched roosts more often (every 1.3 days) than solitary males (every 3.8 days), moved shorter distances, and roosted more often in trees with upper openings than did solitary bats, suggesting that predator avoidance may be an important factor influencing the types of trees that reproductive females use and how often they move among roost trees (Lucas et al., 2015).

Transect surveys during warm months at three study areas with appropriate habitat but differing land use histories (such as habitat disturbance by logging or hot water effluents) in South Carolina yielded 361 trees with basal cavities; 67 of these (19%) had roosting Rafinesque's big-eared bats, including three maternity colonies of 20–35 bats each (Loeb, 2017). Trees with roosts had larger mean diameters and cavity volumes than unused trees, and were in stands with greater tree densities, as well as higher densities and proportions of larger trees than stands with unused trees (Loeb, 2017). Species and cavity types of roost trees varied among study areas along with measures of roost niche breadth: the area with greatest habitat disturbance had broadest niches as defined by several variables except cavity volumes, whereas roost trees at the least disturbed site had larger dimensions in cavity volumes. In general, tree occupancy rates decreased with degree of past habitat disturbance, but the diversity of tree species and forest and wetland types increased, and the influence of cavity attributes of occupied trees and the probability of detecting a roost varied among areas (Loeb, 2017).

Texas**:** Little roost switching was observed in seven radio-tracked Rafinesque's big-eared bats on public lands in the pineywoods ecoregion of eastern Texas, thought possibly due to a low availability of suitable roost trees (Stuemke et al., 2014). In eastern Texas, transect searches and radio tracking of the seven bats showed that compared to unused trees, roost trees (primarily *Nyssa* spp.) had larger diameters and cavities, greater numbers of entrances, and were larger; roost trees also were in trees with entrances higher above ground, and were located in stands with higher numbers of large trees (Stuemke et al., 2014).

Warm Season Roosts in Human-made Structures: Rafinesque's big-eared bats also roost in buildings during the warmer months. As with winter roosts, buildings, bridges, cisterns, and other human-made structures used as roosts can be occupied for multiple years (for example, Hoffmeister and Goodpaster, 1962; Jones and Suttkus, 1975; Clark, 2003; Loeb and Zarnoch, 2011). Multiyear fidelity of Rafinesque's big-eared bat to roost sites in abandoned buildings was documented in eastern North Carolina (Clark, 1990). Differences in temperature, light levels, and disturbance rates between occupied and unoccupied buildings were not found in eastern North Carolina (Clark, 1990). Sealander and Heidt (1990) reported that in Arkansas this bat roosts in dimly lit barn lofts, attics, and old buildings in rural areas, but it is seldom found in caves. Saugey et al. (1989) observed a colony of more than 100 individuals in an abandoned Arkansas school in autumn, a "nuisance" colony of about 65 was reported in the belfry of a church (McAllister et al., 2005), and up to 175 bats (including a maternity colony) intermittently used an Arkansas barn beginning shortly after its construction (Saugey et al., 1993). In southern Illinois, small groups of 30 or fewer have been reported in summer from a house attic and in an old cabin (Hoffmeister, 1989), and small numbers were reported from an attic in western Tennessee (Graves and Harvey, 1974). A maternity colony of several hundred bats roosted in a building in Mammoth Cave National Park in Kentucky (Harvey et al., 1991). In eastern North Carolina, these bats also roosted in darker parts of abandoned buildings but moved to cooler roosts with more light if ambient temperatures in dark sites climbed over about 36ºC (Clark, 1990). Local switching of roost sites among a few nearby buildings was reported in Louisiana, where they were encountered in clusters in summer nursery colonies, typically in partially lighted front areas of roosts (Jones and Suttkus, 1975). Abandoned buildings were used as roosts in Mississippi (including roosts in buildings on or near wildlife refuges), with one roost used by a maternity colony of 62 bats, but no Rafinesque's big-eared bats were found in searches of caves and cisterns (McCartney, 2007).

This species often moves between natural and human-made roosts. Clark (2003) reported that individuals of this species that roost in buildings in a number of southeastern states will shift from buildings to roosts in hollow trees in wetlands. Bats radio tracked in eastern Texas made movements among trees, buildings, or other human-built structures (Stuemke et al., 2014). In south-central North Carolina, Rafinesque's big-eared bats used abandoned structures and hollow trees as roosts about equally, switching roosts every one to two days (Roby et al., 2011). Small numbers also roosted in bridges in southeastern North Carolina (Felts and Webster, 2003). In De Soto National Forest in southern Mississippi, Rafinesque's big-eared bats roosted in human-built structures (including bridges, abandoned houses, and an abandoned oil storage tank) as well as in hollow trees, switching roosts every 2.1 days; half of the 14 maternity roosts discovered were in anthropogenic structures, where fidelity to roosts was higher in the absence of tree roosts (Trousdale et al., 2008). The 25 tracked bats moved between successive roosts that were an average of

573 meters apart (range 120 meters to 4.0 kilometers; Trousdale et al., 2008). In a South Carolina study, Rafinesque’s big-eared bats used anthropogenic structures more often than hollow trees in summer, but not in other seasons; movements among roosts were related to thermal differences among roosts (Loeb and Zarnoch, 2011).

These bats use several different kinds of bridges. Concrete bridges are utilized as diurnal roosts in many areas (Lance et al., 2001; Trousdale and Beckett, 2004; Ferrara and Leberg, 2005a,b; Bennett et al., 2008). In Louisiana, these bats utilize bridges with “double-T” understructures (Lance et al., 2001, Ferrara and Leberg, 2005a,b). Most of the bats found under these bridges were not in colonies but were solitary or roosted in small numbers. These solitary and small groups of Rafinesque’s big-eared bats roosted in microhabitats under these bridges that were warmer and darker than other areas under the same bridge, but about 5ºC cooler than ambient; roosting points also tended to be closer to abutments but far from the edges (Ferrara and Leberg, 2005a). Maternity groups of five to 85 bats roosted under concrete bridges in the Kisatchie National Forest in Louisiana (Ferrara and Leberg, 2005b).

Well over 1,000 bridges were surveyed for Rafinesque’s big-eared bats throughout South Carolina; diurnal roosts of solitary bats or colonies were found at 73 bridges (Bennett et al., 2008). Numbers of bats in colonies fluctuated between repeat visits to bridges within a summer, but colony size ranged from two to 53 with medians of eight to 12 bats in two different summers of surveys. Bats preferred roosting between support beams rather than in expansion joints, and over banks near abutments rather than over water (Bennett et al., 2008). Bats used larger bridges and bridges with T-beam or multiple beam girders rather than slab bridges in South Carolina, and most (95%) bridges with roosting bats were over rivers in the Upper and Lower Coastal Plains physiographic regions rather than in the Piedmont or mountains (Bennett et al., 2008). Investigators determined that bridges should be visited three to five times per year to assure detection of use (Bennett et al., 2008).

McDonnell (2001) surveyed 990 bridges and culverts for use by bats in the Coastal Plain of North Carolina during summers 1997 and 1998. Rafinesque’s big-eared bats were found roosting in 36 of these structures, with 25 of the 36 structures housing solitary bats, several with 2–9 females, and one with a maternity colony of about 40 bats. All but one structure used by these bats were in swamp or bottomland hardwood forest habitats, and only one steel culvert was used, housing a solitary bat. Rafinesque’s big-eared bats were never found roosting under the 105 concrete slab bridges, 87 steel multi-beam bridges, or 65 concrete box culverts investigated (McDonnell, 2001). These bats were found most often under I-beam bridges, followed by channel beam bridges, T-beam bridges, and timber multi-beam bridges. Bridge use was related to degree of disturbance (based on an index of human activity beneath the bridge), but there were no associations between bridges used and average daily vehicle traffic, amount of water under the bridge, age, height, length, or width of the bridge (McDonnell, 2001).

From one to 25 Rafinesque’s big-eared bats were observed under concrete bridges in the DeSoto National Forest in Mississippi during the maternity season, with most solitary bats being adult males and maternity colonies averaging 5.6 ± 3.1 (SD) adult females (Trousdale and Beckett, 2004). Radio-tracking studies revealed that some of these individuals also roosted in hollow trees (Trousdale and Beckett, 2005). In Louisiana, radio-tagged Rafinesque’s big-eared bats switched roosts frequently, also moving between concrete bridges or between bridges and hollow trees; different roost locations of individual bats varied from 70 meters to 2.5 kilometers apart (Lance et al., 2001). During summer Rafinesque’s big-eared bats occupied the same cistern long used as a winter roost in southern Illinois, but roosted in the warm upper portion rather than the lower part used during winter (Hoffmeister and Goodpaster, 1962).

Rafinesque's big-eared bats will use human-made structures specifically built to mimic their natural roosts (Bayless, 2006; see "Management Practices and Concerns" below).

Population Ecology.— Litter Size, Natality, and Female Reproduction: A single young is born (but few primary data are available on litter size) once a year in early summer, following an autumn and winter mating with presumed delayed ovulation and fertilization, although details on the latter processes are lacking (Jones, 1977, Schmidly, 1991). Twelve roosting females were observed with 12 pups under a bridge in Mississippi, where three females were observed giving birth to singletons (Wolters and Martin, 2011). Two of 6 (33%) females netted away from roosts in Arkansas were reproductive (Fokidis et al., 2005). Males apparently do not breed until they are older than one year (Jones and Suttkus, 1975), but little is known about age of first reproduction or inter-birth intervals in females. Sex ratios of young in North Carolina were 1:1 (Clark, 1990). Newborn pups were first observed in mid-May and lactation occurred through mid-to-late July in southern Mississippi, with highest numbers in maternity colonies under bridges occurring in June (Trousdale and Beckett, 2004). In central western Mississippi, parturition was observed in late May (Wolters and Martin, 2011). Similar times for parturition and lactation were noted in eastern Texas (Mirowsky et al., 2004).

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: It has been suggested that a variety of predators, including snakes, raccoons, opossums, and cats may occasionally feed on Rafinesque's big-eared bats (Jones, 1977; Clark, 1990; Clement and Castleberry 2013a,b; see also review in Lacki and Bayless, 2013), but there is little documentation of other factors causing direct mortality in these bats. Rafinesque's big-eared bats are seldom investigated for rabies infections, but rabies-based mortality has been documented (Sasse and Saugey, 2008). An adenovirus has been described from a single bat from Kentucky but without definitive accompanying pathology and mortality (Hackenbrack et al., 2017). A few species of helminth gastrointestinal parasites (McAllister et al., 2005) and ectoparasites are known (Crossley and Clement, 2015), and alopecia (hairlessness) of unknown etiology has been reported (summarized in Lacki and Bayless, 2013), but these cases have not been associated with mortality. There are no published records of multiple mortality events (O'Shea et al., 2016a). The white-nose syndrome fungus has been detected using molecular genetics on the wings of two Rafinesque's big-eared bats sampled at a winter hibernaculum in Tennessee, but no disease or pathology was reported (Bernard et al., 2015). Four Rafinesque's big-eared bats captured away from roosts during summer in Tennessee all were negative by PCR testing of skin samples (Carpenter et al., 2016). It has been suggested that the frequent winter arousals seen in this species may help ameliorate susceptibility to white-nose syndrome and prevent the devastation seen in some populations of eastern bats that experience deeper torpor during hibernation (Johnson et al., 2012b; Bernard et al., 2015). It also has been suggested that if white-nose syndrome pathology occurs in Rafinesque's big-eared bats, it is more likely to be found at the northern portions of their distribution where the bats tend to hibernate longer in caves and at higher densities (Lacki and Bayless, 2013).

A maximum longevity record of at least 10 years has been documented (Paradiso and Greenhall, 1967), and several marked animals survived in a Louisiana colony over an eight-year period (Jones and Suttkus, 1975).

Population Trend: A state-by-state review of survey efforts for these bats was presented by Clark (2003), who noted that regular attempts at monitoring generally had not taken place due to numerous difficulties and challenges. These include frequent switching of roosts and resulting wide fluctuations in numbers from day to day (Clark, 2003; Gooding and Langford, 2004; see also

“Roosting habits” above). Most of the early information on population trends in Rafinesque’s big-eared bats is anecdotal and suggestive of declines or rarity. Belwood (1992:287) stated that in Florida this species “does not seem to be abundant anywhere in the state, is rarely seen, and is uncommon in collections”. Ellison et al. (2003) compiled data from all then-available sources on estimates of colony sizes for Rafinesque’s big-eared bat and found only five colonies with counts on at least four annual occasions. None of these showed significant trends. More recently, 1,138 roosting sites range-wide from 1864 to 2009 have been documented for this species, but this information has not been assessed for trend estimation (Bayless et al., 2011; Lacki and Bayless, 2013).

Jones and Suttkus (1975) noted that when Rafinesque’s big-eared bats are found at scattered locations in the southeast they are mostly in low numbers, and that very few nursery colony locations had ever been reported at the time of their review. Since then nursery colonies of 6–80 adult females were documented in eastern North Carolina, where one past colony may have been as high as 300 (Clark, 1990); one colony of “several hundred” is known from a building in South Carolina (Menzel et al., 2003:132). Other more recent efforts have found additional nursery colonies in multiple areas throughout the distribution (see “Roosting habits” above), with maximum colony sizes of 80–100 reported in hollow trees (Clark, 1990, 2003; Lance et al., 2001; Gooding and Langford, 2004; Johnson et al., 2012a; Lucas et al., 2015) and 118 in a cave (Hurst and Lacki, 1999). A total of 700–800 Rafinesque’s big-eared bats were counted at 13 maternity colony sites in Mammoth Cave National Park in Kentucky (Bayless et al., 2011). Forty-two roosting sites in a variety of bridges, buildings, and hollow trees in Mississippi during 2001–2009 held maternity colonies ranging in size from four to 160 bats, with the latter group sharing four roost trees (Trousdale et al., 2008; Martin et al., 2011).

The largest known winter concentrations of these bats occur in 10 hibernacula in the Appalachian Mountains and central plateau of Kentucky, North Carolina, and Tennessee, where about 4,100 Rafinesque’s big-eared bats have been counted in winter (Bayless et al., 2011). Sasse et al. (2011) provide winter count data of Rafinesque’s big-eared bats at 37 abandoned wells used as hibernacula in Arkansas (maximum count of 103 at one well) that suggest a decline over a 21-year period of observation. A search of 21 caves in the Alabama coastal plain during winter 1988 resulted in observations of just two individuals in one cave; only one bat was found during a subsequent visit in 1990 (Best et al., 1992). Rafinesque’s big-eared bats were not found in searches of 22 caves in Mississippi during 2005–2007 (McCartney, 2007), but a winter roost in a tree cavity in Mississippi held over 200 individuals (Stevenson, 2008).

Increased efforts over the past decade have allowed more quantitative estimation of the probability of detecting colonies of these bats (see also “Roosting habits” above). In Mississippi, Fleming et al. (2013b) estimated that searches for roost trees of both this species and the southeastern myotis had detection probabilities above 90%, but that visual estimates of colony size by inspecting internal cavities underestimated numbers of bats compared to digital imagery, with increased error in larger colonies. Comer et al. (2014) compared detection probabilities for Rafinesque’s big-eared bats using acoustic sampling versus roost search transects in eastern Texas piney woods habitat and found that 18 nights of acoustic surveys (using two detectors) would yield a detection probability of 90%, whereas 56 one-kilometer length transects would be required to attain the same detection probability.

In contrast, Clement and Castleberry (2011) reported that detection of Rafinesque’s big-eared bats in their Georgia study region was more cost-effective using roost surveys, followed by mist netting, with acoustic surveys least cost-effective. Clement and Castleberry (2013d) estimated abundance and density of colonies of Rafinesque’s big-eared bats across eight study sites in floodplain forests in Georgia using a modeling approach that combined results of transect surveys for roost trees with landscape-level habitat variables. They found that colony density on eight separate study sites was predicted by duration of flooding, wetland width (narrower widths characterized deeper sloughs which favor trees with characteristics of higher use by bats), and site-specific characters. Over combined study sites (greater than 16,000 ha) the model estimated a mean of 3,734 "colonies" containing an estimated 6,910 adult bats (Clement and Castleberry, 2013d). This quantitative approach provides at the least a more optimistic outlook on the numbers of these bats that may exist range-wide.

Population Genetics: Genetic diversity measures were calculated for Rafinesque's big-eared bats based on mitochondrial DNA control region sequences for 360 individuals from about 31 localities in nine states (Piaggio et al., 2011). Overall genetic diversity was high (haplotype diversity and to a lesser extent nucleotide diversity), and two finer-scale measures of genetic diversity were higher in Arkansas, Texas, and Louisiana colonies than in colonies sampled in North Carolina, Mississippi, and Tennessee (Piaggio et al., 2011). Genetic structuring was evident across five well-sampled colonies in Arkansas. Assessment of genetic diversity was also made for these five colonies based on 10 microsatellite loci. Average number of alleles per locus was 7.7 (range two to 16); in contrast to mitochondrial DNA findings, microsatellite diversity was considered low in these Arkansas colonies, structuring was evident among colonies, and effective colony sizes also were low, but little evidence of inbreeding was detected (Piaggio et al., 2011)

MANAGEMENT PRACTICES AND CONCERNS.— Based on population genetic assessments of phylogeny, management of Rafinesque's big-eared bats based on past subspecies status (Handley, 1959) is not recommended (Piaggio and Perkins, 2005; Piaggio et al., 2011). Consideration of management actions to increase genetic connectivity among colonies in Arkansas was suggested by Piaggio et al. (2011). Jones (1977) regarded this species as highly susceptible to disturbance because of its habit of roosting in places likely to attract people, such as caves, mines, and vacant buildings. Forested areas and old buildings are being altered or destroyed as a result of changing land-use patterns, with likely negative consequences for Rafinesque's big-eared bat in many parts of the southeastern U.S. (Belwood, 1992). Clark (1990) reported reduced activity and abandonment of roosting sites in abandoned buildings coincident with logging of adjacent forests in North Carolina, and documented that logging made the buildings more conspicuous and thus more prone to disturbance and vandalism. Both reduction in bat numbers and rapid roost structure deterioration were noted over the course of a 14-year survey of buildings in North Carolina (Clark, 2003). However, there are occasional reports of colonies persisting in barns that were actively used by people (Clark, 1990).

Identification and protection of manmade structures used as roosts are important actions for conservation of Rafinesque's big-eared bats (Miller et al., 2011; Lacki and Bayless, 2013). Sasse et al. (2011) found that multiple abandoned wells used as winter roosts in Arkansas were likely to be closed because of safety and environmental regulations, so they designed covers that allow bats to fly in and out yet block human access (Sasse and Saugey, 2014). Lance et al. (2001) found that the older concrete bridges with girders selected as day roosts by Rafinesque's big-eared bat in the Kisatchie National Forest in Louisiana are being replaced by concrete bridges with flat bottoms. This type of construction is not favored by this species for roosts; therefore Lance et al. (2001) suggested that the replacement bridges could be modified with the addition of structures that would provide secure roosts. Changes in structures of bridges favored by Rafinesque's big-eared bats on De Soto National Forest in Mississippi were also noted by Trousdale and Beckett (2004), who documented occupancy of these sites by breeding females and young. They suggested that timing for replacement of these bridges take place outside of the maternity season. Darkness was an important factor in selection of roosting areas under bridges by these bats in Louisiana, prompting the recommendation that vegetation removal around these structures be restricted to avoid increasing light penetration (Ferrara and Leberg, 2005a).

In many areas the natural roosts favored by this species are in hollow trees in or near bottomland hardwood forests, more frequently in live trees rather than snags (Clark, 2003; Gooding and Langford, 2004; Trousdale and Beckett, 2005; see above and review by Trousdale, 2011). Studies in Georgia emphasized that management practices that retain and recruit large trees with large internal cavities in flooded areas are critical for maintaining roosting populations of this species in bottomland hardwoods (Clement and Castleberry, 2013c). Anecdotal observations in Texas have documented that roost trees used by Rafinesque's big-eared bats can be destroyed in severe storms and hurricanes (Stuemke et al., 2014).

A detailed overview of the likely impacts of forest habitat loss and degradation on Rafinesque's big-eared bat is available in Lacki and Bayless (2013). In general, the bottomland hardwood forests of the southeastern U.S. have suffered marked declines since historic times, and this has likely impacted populations of Rafinesque's big-eared bats throughout their distribution (for example, Twedt and Loesch, 1999; see also Clark, 2003 for review). In Louisiana, maintenance of mature deciduous forest is considered important for conservation of Rafinesque's big-eared bat, particularly black gums, water tupelos, and other trees that form hollows suitable as day roosts (Lance et al., 2001; Gooding and Langford, 2004). Retention of large-diameter, hollow trees with large cavities has also been recommended in South Carolina (Lucas et al., 2015; Loeb, 2017), as has been management that promotes the recruitment and survival of tree species that eventually form large cavities (Trousdale, 2011; Loeb, 2017). Based on studies in South Carolina, Loeb (2017) also recommended that in areas with the least history of habitat disturbance, preservation of tupelo and bald cypress trees will be most beneficial for maintaining roosting trees on the landscape, whereas in areas with a history of greater habitat change preservation of large oaks, sweetgums, sycamores, and beech trees is also suggested. In Mississippi, Stevenson (2008) recommended that in particular American beech, American sycamore, black tupelo, sweetgum, and bald cypress trees should be retained in forest stands for cavity production. Trousdale (2011) also recommended that in addition to retention of suitable roost trees, management should also consider protecting associated stands so that removal of surrounding trees does not result in altered microclimates of roost trees.

In a preliminary assessment of the availability of natural roosting habitat for Rafinesque's big-eared bat, Miller et al. (2011) calculated areal coverage of bottomland hardwoods with water tupelo trees more than 50 centimeter girth within the Coastal Plain of nine Southeastern States in 2010. The three states with the greatest potential habitat were Louisiana (90,000 ha, 89% privately owned), Florida (56,000 ha, 25% privately owned), and North Carolina (35,000 ha, 89% privately owned). Overall potential habitat totaled 309,000 ha, with 72% privately owned (Miller et al., 2011). Clearly future conservation and management for this species will require cooperation and partnerships involving private entities.

In upland forests in the Daniel Boone National Forest in Kentucky, the U.S. Forest Service has developed a "Cliffline Management Policy" (Lacki, 1996:42) designed to benefit this species, as well as the endangered Virginia big-eared bat, *Corynorhinus townsendii virginianus*. This policy affords full protection to a 92 meter-wide strip of forest, 61 meters below and 31 meters above cliffs within the known range of Virginia big-eared bats and within 1.6 kilometers of any known roosts of Rafinesque's big-eared bats, and further prohibits timber harvest within a 0.4 kilometers radius 'no-disturbance zone' around any such roost (Lacki, 1996, p.42). As pointed out by Hurst and Lacki (1999), the 0.4–kilometer radius zone is probably adequate to sustain microclimates around roosts, provide cover for foraging bats, and provide foraging habitat for newly volant young, but additional management zones should be extended to at least 2.5 kilometers around known roosts to protect foraging habitat of adults.

Disturbance by investigators during periodic monitoring of use of bridges by Rafinesque's big-eared bats does not seem to affect subsequent use of these sites in Louisiana, situations wherein colonies are small and bats are easily seen (Ferrara and Leberg, 2005b). However, because of frequent roost switching and temporary absences of bats, the research in Louisiana showed that at least three surveys during summer were necessary to have a less than 10% chance of misidentifying a roost bridge as not being used. Other investigators determined that bridges should be visited three to five times per year to assure detection of use (Bennett et al., 2008). Rafinesque's big-eared bats will accept certain gate designs at mouths of abandoned mines, and gated mines house some of the largest known hibernating colonies of this species (Burghardt, 2000).

Rafinesque's big-eared bats will use manmade structures specifically built to mimic their roosts (Bayless, 2006). Cinder-block towers (4.3 meters tall) were used at Trinity River National Wildlife Refuge in Texas, with bat use of specific towers apparently varying with seasonal thermal preferences (Bayless, 2006). Artificial roosts constructed by stacking concrete culverts to mimic hollow trees have been successfully colonized by Rafinesque's big-eared bats at St. Catherine Creek National Wildlife Refuge in Mississippi, where one roost was used as a maternity colony by about 30 bats in 2006 (McCartney, 2007; Martin et al., 2011). On Noxubee National Wildlife Refuge in Mississippi, artificial roosts made of up-ended steel culverts were observed to be used by these bats in spring and autumn (Stevenson, 2008; Martin et al., 2011). Also at Noxubee National Wildlife Refuge, the U.S. Fish and Wildlife Service has added openings to trees with cavities that had no previous access points for bats: Rafinesque's big-eared bats have been observed subsequently using these trees as roosts (Richardson, 2007). Given the large degree of roost switching used by these bats, protection and management of areas with tracts large enough to support multiple roosts is important.

Because the diet of this species has a high composition of lepidopterans, concern exists for possible impacts on the food supply due to forest insecticide treatments against pest moths (Lacki and Bayless, 2013).

Notes and Comments.— Several important research papers on *C. rafinesquii* appear in the volume edited by Loeb et al. (2011a), including literature reviews pertinent to their conservation and management (for example, Loeb et al., 2011b; Miller et al. 2011). Bat Conservation International and the Southeastern Bat Diversity Network have developed a conservation and management plan for Rafinesque's big-eared bat and the southeastern myotis (Lacki and Bayless, 2013) that reviews additional detailed biological information, major threats and conservation needs, and provides well-considered specific suggestions for future research and conservation strategies. The major past, present, and future threats identified include those noted above, and are grouped as: loss and degradation of bottomland hardwood forest; altered hydrology; climate change; loss and degradation of mature upland forest; loss of natural roosting habitat; loss of anthropogenic roosting habitat; disturbance at roosting sites; disease; white-nose syndrome; wind energy development; air strikes; loss of genetic diversity; and insufficient conservation planning. Areas of needed actions discussed in the document (Lacki and Bayless, 2013) include further identification of occupied habitat and roost sites, protection and creation of roosts, development and implementation of population inventory and monitoring methods, population genetics research, management of foraging habitat, monitoring for new and emerging threats, education and outreach, development of conservation incentives, and recommendations for research.

Corynorhinus townsendii — Townsend's big-eared bat (Family Vespertilionidae)

Conservation Status.— The federal conservation status of Townsend's big-eared bat varies with subspecies (see "Distribution and Systematics" below). The Virginia big-eared bat (*C. townsendii virginianus*) and the Ozark big-eared bat (*C. townsendii ingens*) subspecies are listed as Endangered (U.S. Fish and Wildlife Service, 1979) and are not considered in detail in this account. Conservation status designations for the species exclusive of the Ozark and Virginia subspecies are given below.

National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. Bureau of Land Management (2009a,b, 2010a,b,c, 2011a,b, 2015a,b, 2017): Sensitive Species (Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Utah, Washington, Wyoming state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Species Rounded Global Status G4, Apparently Secure; subspecies *C. townsendii townsendii* and *C. townsendii pallescens*: Rounded Global Status T3, Vulnerable.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need, *C. townsendii pallescens*. California Division of Fish and Wildlife (2015a,b,c): Candidate for listing as state Threatened, Special Animals List, Species of Special Concern. Colorado Parks and Wildlife (2015a, 2015b): State Special Concern, Species of Greatest Conservation Need Tier I, *C. townsendii pallescens*. Idaho Department of Fish and Game (2005, 2015): Species of Greatest Conservation Need Tier 3. Kansas Department of Wildlife, Parks and Tourism (2005; Rohweder 2015): Species of Greatest Conservation Need Tier I (designated in 2005), Tier II (designated in 2015). Montana Fish, Wildlife, and Parks (2005, 2015a,b): Species of Greatest Concern, Species of Greatest Conservation Need. Nebraska Game and Parks Commission (2011): Tier II At-Risk Species. Nevada Department of Wildlife (2013): Sensitive Mammal. Nevada Department of Conservation and Natural Resources (2015a): Imperiled. North Dakota Game and Fish (Dyke et al., 2015): Species of Conservation Priority Level I. Oklahoma Department of Wildlife Conservation (2005, 2016): Species of Greatest Conservation Need Tier II, *C. townsendii pallescens*. Oregon Department of Fish and Wildlife (2005, 2008) Sensitive Species, Critical. South Dakota Game, Fish, and Parks (2014): Species of Greatest Conservation Need. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need, *C. townsendii australis*. Utah Division of Wildlife Resources (2015; Sutter et al., 2005): Species of Greatest Conservation Need. Washington Department of Fish and Wildlife (2015a,b): Species of Concern, Candidate for State Listing as Threatened or Endangered, Species of Greatest Conservation Need. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier II.

Description.— Townsend's big-eared bat (Fig. 9) is fairly distinctive among U.S. bats based on the very large ears, which are similar only to those of Rafinesque's big-eared bat, the spotted bat, and Allen's big-eared bat. Pelage coloration in Townsend's big-eared bat varies from pale cinnamon to blackish brown at the hair tips dorsally, and brownish or buff ventrally (Kunz and Martin, 1982). The spotted bat has a blackish dorsal pelage with large white spots, in contrast to the more uniform brownish-gray coloration of Townsend's big-eared bat. Allen's big-eared bat, found only in the southwestern U.S., has a similar pelage to the Townsend's big-eared bat but differs in that it has a "lappet", or fleshy lobe extending across the forehead between the ears. Townsend's big-eared bat has two large lumps (pararhinal glands) on the face between the nostrils and the eyes. Rafinesque's big-eared bat, found primarily in the southeastern U.S., is most similar to Townsend's big-eared bat, but has sharply contrasting color differences between the bases and

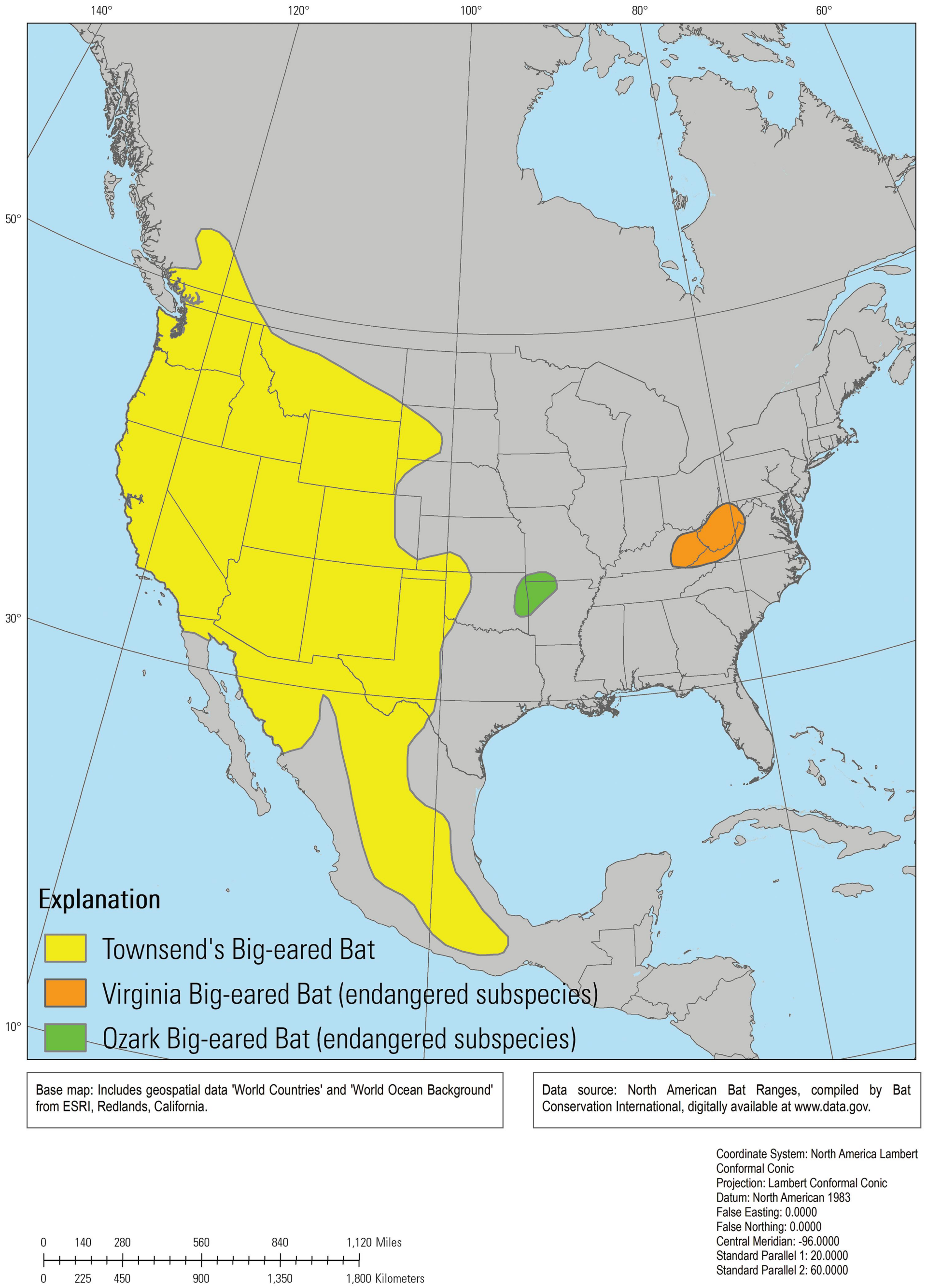
FIGURE 9. Townsend's big-eared bat, *Corynorhinus townsendii* (photo by J. Scott Altenbach).

tips of the hair on the venter (Jones, 1977). Hairs on the feet extend beyond the tips of the toes in Rafinesque's big-eared bat but not in Townsend's big-eared bat (Sealander and Heidt, 1990). Adult body mass of Townsend's big-eared bats ranges from five to 13 grams; females may average slightly larger than males, and reportedly reach heavier body mass in autumn and winter (as summarized by Kunz and Martin, 1982; Ingersoll et al., 2010). The calcar is not keeled. This species often curls its ears backwards in a manner resembling ram's horns when hibernating or torpid.

DISTRIBUTION AND SYSTEMATICS.— Five recognized subspecies of Townsend's big-eared bat occur within the U.S. (Handley, 1959; Kunz and Martin, 1982). Two isolated subspecies in the eastern and central U.S. were listed as Endangered under the U.S. Endangered Species Act in 1979 (U.S. Fish and Wildlife Service, 1979): the Virginia big-eared bat occurs in parts of West Virginia, Virginia, Kentucky, and North Carolina; the Ozark big-eared bat is found or historically occurred in restricted limestone areas of adjacent portions of Arkansas, Oklahoma, Missouri, and Kansas. The isolated distributions of the Ozark big-eared bat and Virginia big-eared bat were thought to be relicts of post-Pleistocene climates (Humphrey and Kunz, 1976), but more recent genetic analysis suggests a much older divergence (Piaggio and Perkins, 2005; Lack and Van Den Bussche, 2009).

Overall, the remaining three U.S. subspecies are found across the western and west-central states (Fig. 10). The subspecies distributions described by Handley (1959) and provided in the range descriptions in the 1994 designation of federal Category 2 candidates (U.S. Fish and Wildlife Service, 1994) have changed based on modern phylogenetic analysis (Piaggio and Perkins, 2005; Smith et al., 2008; Lack and Van Den Bussche, 2009; Piaggio et al., 2009). *C. townsendii townsendii* occurs in the lower 48 states from the Pacific coast east to southern Montana, western South Dakota, western Colorado, and western New Mexico; *C. townsendii pallescens* occurs from western Colorado and northeastern Arizona eastward through south-central Wyoming to western Kansas, western Oklahoma, and northwestern Texas; *C. townsendii australis* is found in western Texas, southern New Mexico, and Mexico (see Lack and Van Den Bussche 2009 for map; Tipps 2012). These three subspecies are not practical to distinguish in the field (Pierson et al., 1999).

Improved knowledge about systematic relationships of the bats in the big-eared bat subgroup (including *Corynorhinus*, *Euderma*, *Idionycteris*, and *Plecotus*) within the family Vespertilionidae have resulted in changes in nomenclature within the past 25 years. These changes have caused some confusion for the non-specialist. As summarized by Tumlinson and Douglas (1992) and Bogdanowicz et al. (1998), the names *Corynorhinus* and *Idionycteris* are now the generally accepted generic names for U.S. bats formerly grouped under the genus *Plecotus* (including the species previously known as *Plecotus townsendii*, *Plecotus rafinesquii*, and *Plecotus phyllotis*). The generic name *Plecotus* remains valid only for certain species of Old World bats. Previous nomenclature was largely based on morphological studies that were concluded in the 1950's (Handley, 1959),



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 10. Approximate distribution of Townsend's big-eared bat, *Corynorhinus townsendii*.

which placed *Corynorhinus* and *Idionycteris* under the genus *Plecotus*. Prior to this effort, however, *Corynorhinus* had been accepted as a correct generic name. Therefore, in the scientific literature of the past century the reader may find reference to Townsend's big-eared bat as *C. townsendii* prior to about 1960, *P. townsendii* during the decades of the 1960's-1980's, and *C. townsendii* again since the 1990's. The literature prior to the early 1960's is further confounded by the now-incorrect application of the name *C. rafinesquii* (or *P. rafinesquii*) to *C. townsendii*, or the designation of Townsend's big-eared bat as *C. rafinesquii townsendii*. Currently, however, *C. rafinesquii* remains the appropriate species name solely for Rafinesque's big-eared bat in the southeastern U.S. These changes reflect continual refinements and progress in understanding the systematic and evolutionary relationships of bats. Genetic analysis using nuclear DNA sequences and mitochondrial DNA analysis affirm the relationships among the species of *Corynorhinus* and the subspecies of Townsend's big-eared bat (Piaggio and Perkins, 2005; Piaggio et al., 2009; Lack and Van Den Bussche, 2009; Tipps 2012). See Kunz and Martin (1982) for a taxonomic synonymy of past scientific names applied to Townsend's big-eared bat prior to the more recent changes noted in the above references.

The generic name *Corynorhinus* stems from Greek words meaning "club" and "nose". This bat is named in honor of John Kirk Townsend, an American naturalist and collector during the early 1800's (not Charles H. Townsend, a later naturalist, as attributed by Kunz and Martin, 1982). Other English common names include western lump-nosed bat, western long-eared bat, western big-eared bat, western long-nosed bat, long-eared bat, jack-rabbit bat, and mule-eared bat.

Habitats and Relative Abundance.— In the western U.S., Townsend's big-eared bats are found in a wide variety of habitats, ranging from arid desert lowlands to fir forests (for example, Dalquest, 1947a; Easterla, 1973; Findley et al., 1975; Ports and Bradley, 1996; Szewczak et al., 1998). However, they are usually restricted to areas within these habitats that provide roosts in caves, or cave-like structures such as mines, large rock crevices or cavities, and some bridges and buildings (see "Roosting Habits" below). This species is often among the least abundant captured in mist-netting surveys. Low relative abundance may be a reflection of rarity, but it could be attributable in part to capture bias if their maneuverability and echolocation abilities allow them to avoid nets more readily than other species (for example, Cockrum and Ordway, 1959) and because they may not move far from limited roosting habitat. These factors of detectability may negatively bias relative abundance data. Positive bias to relative abundance data may also occur when observations are based on counts at roosts if this species is more dependent on open and conspicuous (observable) roosting sites within caves and mines where bats are often sought.

Pacific Northwest and Northern Rocky Mountains: *Oregon and Washington*: Only one Townsend's big-eared bat was captured in surveys over streams and ponds in Douglas fir-western hemlock forests across the western Cascades in southern Washington and the Oregon Coast Range, ranking last among 12 species and 241 individuals captured (Thomas, 1988). Similarly, they were the least abundant of 11 species collected for stomach contents analysis in eastern Oregon, with one bat taken among a sample of 413 individuals (Whitaker et al., 1981), and they were the least abundant (one capture out of 1,057 individuals of 11 species) among bats captured over water in the predominantly ponderosa pine forests of the eastern Cascade Mountains of south-central Washington (Baker and Lacki, 2004). However, Townsend's big-eared bats ranked fourth of eight species (five captured among 412 individuals) of bats captured night roosting at five bridges in western hemlock forest in the Willamette National Forest of Oregon (Perlmeter, 1996).

***British Columbia*:** One Townsend's big-eared bat was captured over water in the semi-arid Okanagan Valley of southern British Columbia, where the species ranked as least abundant of 12 species documented through capture of 958 individuals (Woodsworth, 1981). None were captured in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water, although one was captured at a talus slope away from water (Fenton et al., 1980).

***Idaho and Montana*:** None were documented among 187 bats of eight species captured in mist nets set over water in forests of multiple types in northern Idaho (Lacki et al., 2007). None were taken among 205 bats of seven species netted or shot over water at beaver ponds and in nearby ponderosa pine forest in the Long Pine Hills and Ekalaka Hills of southeastern Montana, at elevations of 1,036–1,158 m (Jones et al., 1973). Although they were captured in caves in the region and are widely distributed in Montana (Hoffmann et al., 1969), Townsend's big-eared bats were not detected in netting over water in the Pryor Mountains of south-central Montana, where nine other species and 231 individuals were taken (Worthington, 1991).

California and Nevada: In California, the two most important determinants of distribution were thought to be the availability of roosting sites and the degree of human disturbance at the roosts (Pierson and Rainey, 1998a; see also: Pearson et al., 1952; Graham, 1966). Townsend's big-eared bat ranked fourteenth out of 17 species (three individuals among 390 bats) captured in mist nets during 1993–1999 at 19 sites over a range of elevations in the Sierra Nevada Mountains of California, including Yosemite National Park (Pierson et al., 2001). Along montane areas around the upper Sacramento River in northern California, this was the least frequently captured of 15 species taken in mist nets set over water, with one bat documented among 1,398 individuals captured during four summers (Pierson et al., 1996b). They were also the least abundant bat observed using bridges as night roosts in montane hardwood and conifer habitats along the upper Sacramento River (elevations 320–730 meters), with two bats captured among 2,132 individuals of nine species documented using these structures at night (Pierson et al., 1996b). In the Mojave Desert, these bats were least abundant (three captures) among 6 species and 439 individuals sampled over water or nearby flyways at Fort Irwin National Training Center (Grinnell et al., 2012).

Townsend's big-eared bats were not documented in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests, and 403 bats of 10 other species were captured (Duff and Morrell, 2007). They also were not documented in a mist-net survey both over water and within forests (concentrating on groves of giant sequoia trees, *Sequoiadendron giganteum*) in Yosemite National Park in the California Sierra Nevada Range, where 10 other species and 284 individuals were captured (Pierson et al., 2006). A survey based on mist netting over water in old-growth redwood forest in the Coast Range of northern California failed to document this species among 142 bats of seven species captured (Zielinski and Gellman, 1999).

In the White and Inyo Mountains of Nevada and California, where they were taken in upper Mojave and Great Basin desert scrub through piñon-juniper woodland habitats, Townsend's big-eared bats were low in abundance (three captures), ranking about twelfth of about 2,000 bats of 13 species netted over water (Szewczak et al., 1998). Thirteen individuals were captured among 1,345 bats of 13 species (ranking fifth) documented in mist nets set over very small watering sources in multiple habitats (but mainly desert scrub) at the Desert National Wildlife Refuge in Clark County, southern Nevada, an area that includes abandoned mines (O'Farrell and Bradley, 1970; O'Shea et al., 2016b). Hall (2000) documented the species in Great Basin desert habitats on the Nevada Test Site in south-central Nevada, ranking eleventh with 11 captures among 2,099 individuals of 13 species sampled over water. These bats ranked fourth (24 captures among 299 bats of 11 species) in mist-netting surveys over water in west-central Nevada in habitats categorized as desert shrub and piñon-juniper woodland zones; this area included abandoned mines used as roosts by this species (Kuenzi et al., 1999). In the same general region of Nevada, radio-tracked Townsend's big-eared bats tended to spend more time foraging in piñon-juniper habitat compared to its availability on the landscape (Ives, 2015).

In eastern Nevada, mist netting over water and captures at abandoned mines and tunnels in six habitat zones documented the occurrence of this species throughout the region, particularly in juniper-covered foothills, caves, and river canyons with high cliffs in a variety of habitat types (Ports and Bradley, 1996).

Southwestern U.S.: ***Arizona*****:** Townsend's big-eared bats ranked seventh in relative abundance (214 captures among 3,458 individuals) of 17 species netted over water in Mohave County in northwestern Arizona, where they were captured at sites in multiple habitat types (Cockrum et al., 1996). At Kofa National Wildlife Refuge in southwestern Arizona, they ranked fifth of 6 species documented drinking at small artificial water sources in lower Colorado River Sonoran and Arizona Upland Sonoran Desertscrub vegetation types, with 22 individuals captured among 427 bats (Rabe and Rosenstock, 2005). They were the least frequently captured bat in ponderosa pine forests at about 2,200 to 2,600 meters elevation on the Coconino Plateau in northern Arizona (two captured among 1,673 bats of 15 species; Morrell et al., 1999). This species ranked seventh in abundance among 17 species of bats (46 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). They were not documented among 353 individuals of 15 species captured in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim, on the Tonto National Forest in central Arizona (Lutch, 1996).

New Mexico**:** Townsend's big-eared bat was the least abundant species taken in mist nets in the Jemez Mountains in north-central New Mexico during the 1990s, where capture sites spanned elevations between 1,753 and 2,774 meters and ranged from piñon-juniper woodlands to spruce-fir forests (seven captures among 1,532 bats of 15 species), with echolocation activity detected only in riparian and piñon-juniper habitats (Bogan et al., 1998; Ellison et al., 2005). Also in northern New Mexico, these bats were not documented among 302 bats of 10–11 species netted in mostly ponderosa pine habitat on Mount Taylor during 2006 and 2007 (Geluso, 2008).

Three studies assessed the relative abundance of bats at various locations in the San Mateo Mountains of west-central New Mexico. No Townsend's big-eared bats were captured in netting over several stock ponds in ponderosa pine forest, where a total of 447 bats of seven to eight species were documented (Chung-MacCoubrey, 2005). One was captured among 855 individuals of 16–17 species captured during 1970 at Nogal Canyon, Socorro County, in habitats described as pinyon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974). The species ranked ninth in relative abundance (eight captured among 1,390 bats and 11 species) during 19 summers of netting during the period 1971–2005, at a pond in ponderosa pine/mixed pine forests at an elevation of 2,573 meters in Bear Trap Canyon, Socorro County (Geluso and Geluso, 2012). None were captured in a survey documenting six species and 130 individuals netted over water along the middle Rio Grande in the Bosque del Apache National Wildlife Refuge in central New Mexico (Chung-MacCoubrey, 1999), although an individual was taken at a roost at a building on the refuge (Valdez et al., 1999b). They were low in relative abundance (a total of 35 among 1,595 bats of 20 species captured, ranking thirteenth) in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were most often captured in woodlands and evergreen forest above 1,524 meters (Jones, 1965). Similar relative abundance and habitats were reported in a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling (Jones and Suttkus, 1972). Somewhat farther south, Jones (2016) documented bats captured during surveys of the Greater Gila region of Catron, Grant, and Sierra counties; this species ranked second-to-least abundant, with two taken among 282 captures of 16–17 species (Jones, 2016). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species, with one Townsend's big-eared bat captured, ranking lowest in relative abundance (Geluso, 2006, 2017).

***Texas*:** In Big Bend National Park in Texas, Easterla (1973, p.96) described this species to be “fairly common”, ranking fourth in relative abundance throughout the park (496 among 4,807 bats captured of 18 species at 32 localities, but including 296 captures at roosts; Easterla, 1973). They were rarely captured and ranked 13th in relative abundance (17 captures among 1,978 bats) of 17 species in a subsequent study during 1996–1998, which emphasized surveys over water in lowland habitat at the park; all captures in the latter study were in rocky canyons (Higginbotham and Ammerman, 2002). Townsend’s big-eared bats ranked eighth out of 14 species (nine among 542 individuals) captured by mist net sampling at 108 localities over water in northern Chihuahuan desert habitats described as desert scrub, desert grassland, riparian, and juniper roughland at Big Bend Ranch State Park, northwest and upstream of the national park, in the Trans-Pecos region of Texas; capture records only were in riparian woodland habitat (Yancey, 1997). They were low in relative abundance (three captures among 1,329 individuals in 12 species, ranking tenth) captured in mist nets set over water at Palo Duro Canyon State Park in the Texas Panhandle, where habitats consisted of mesquite (*Prosopis glandulosa*)-juniper associations, grasses, cacti, and a riparian zone of cottonwood (*Populus deltoides*) and salt cedar (*Tamarix ramosissima*) set within sandstone, shale, and limestone canyon walls (Riedle and Matlack, 2013).

Central Rocky Mountains and Western Great Plains: *Colorado*: Townsend’s big-eared bats ranked twelfth (13 captures among 1,996 bats of 15 species) in predominantly piñon-juniper woodland habitat at Mesa Verde National Park in southwestern Colorado during 2006 and 2007 (O’Shea et al., 2011a). In an earlier study at Mesa Verde National Park during 1989–1994, they ranked third most abundant (20 bats among 189 individuals in 11 species; Chung-MacCoubrey and Bogan, 2003). Differences in relative abundance between the two studies were probably due to greater selection of smaller pools of water for netting during the earlier work: small pools were less available during the 2006–2007 study but were likely more easily approached for drinking by the highly maneuverable Townsend’s big-eared bat than by many other species (O’Shea et al., 2011a). This species ranked tenth in abundance among 11 (five out of 546 bats) captured over stock ponds during surveys in piñon-juniper woodland at about 2,100 meters elevation in the Uintah Basin of Moffat County in northwestern Colorado during 1979–1981 (Freeman, 1984). Townsend’s big-eared bats ranked eighth among 10 species (12 captures out of 1,398 individuals) taken in ponderosa pine and Douglas fir forests along the Colorado Front Range in Boulder County (Adams et al., 2003) and were the least abundant of nine species in a second survey in the mountains of adjacent Larimer County, with one bat captured among 634 individuals (O’Shea et al., 2011b). In western Colorado, this species was ranked twelfth of 16 species (seven captured among 899 bats) documented at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). They ranked tenth in abundance (43 captures among 1,377 bats of 15 species) in mist-netting surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

***Utah*:** In northern Utah, mines and caves used by this species tended to be at lower elevations in sagebrush grassland, juniper woodland, and mountain brush vegetation communities; a number of other surface habitat variables were measured and contrasted but did not show significant differences between occupied and unoccupied sites (Sherwin et al., 2000). At Arch Canyon on the Colorado Plateau in southeastern Utah, this was among the least abundant species, with two bats captured among 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016). Similarly, they ranked tenth of 15 species in relative abundance (16 captures among 572 individuals) in the Henry Mountains of southeastern Utah, where habitats and elevations of capture sites where this species was taken ranged from 1,295 to 2,396 meters (Mollhagen and Bogan, 1997).

***Wyoming*:** Townsend's big-eared bats ranked tenth of 12 species in relative abundance (four captured among about 370 individuals) documented by mist netting in lower elevation basin and foothills habitat during 2012 in the south-central part of Wyoming (Abernethy et al., 2013). They were not documented among 246 bats of six species captured in mist net surveys over streams and beaver ponds in and near the Medicine Bow National Forest in southern Wyoming, at elevations ranging from 2,133 to 2,896 meters and in habitats encompassing lodgepole pine (*Pinus contorta*) and spruce-fir forests (Gruver, 2002).

***South Dakota*:**. This was the third most common species in sampling at Badlands National Park in South Dakota, with 43 captured among 405 bats of nine species (Bogan et al., 1996; but see also Farney and Jones, 1980, where they were found to be least abundant in the same park). Townsend's big-eared bats were not documented among seven species and 1,197 individuals of bats captured during warm seasons in ponderosa pine-dominated habitat in the Black Hills of South Dakota (Cryan et al., 2000), where hundreds hibernate during winter in nearby Jewel Cave (Choate and Anderson, 1997). Similarly, just one was captured among 209 individuals of nine species in mist nets set over water during summer 1989 near Jewel Cave (Choate and Anderson, 1997), but a maternity colony at the southern periphery of the Black Hills was found through re-visitation of several low-elevation sites where disparate records of reproductive females had been previously reported (Cryan, 1997).

FORAGING AND DIETARY ANALYSIS.— Foraging habitat use in this species is likely to be variable. Acoustic sampling in the western hemlock forest zone of the Cascade Mountains in Washington found that Townsend's big-eared bats did not use mature stands but were detected most often in clearcuts (both habitats had lower indices of use for this species than for other species of bats; Erickson and West, 1996). Light-tagged Townsend's big-eared bats observed in western Oklahoma shortly after emergence foraged closer to canyon walls and lower to the ground than other local species of bats, sometimes foraging within patches of streamside vegetation, and occasionally stopping to rest on rock faces (Caire et al., 1984). Limited observation by telemetry in central Oregon suggested that foraging activity was greatest in more open habitats in shrub steppe and ponderosa pine forest-shrub ecotones (Dobkin et al., 1995). It has been suggested that these bats may favor edge habitats in Utah, particularly interfaces between juniper woodlands and sagebrush-grassland steppe (Sherwin et al., 2000), whereas in western Nevada foraging bats used piñon-juniper woodlands greater than availability of that habitat on the landscape (Ives, 2015). Occasional winter foraging by this species has been documented in Colorado (Ingersoll et al., 2010).

A small sample of female Townsend's big-eared bats radio tracked during spring and early summer in southeastern Idaho, prior to formation of maternity colonies, foraged in areas ranging from 24 to 61 hectares in the interface between sagebrush-steppe and juniper woodland, with foraging areas less than 0.8 kilometers from night roosts (Haymond, 1998). Radio-tracking studies conducted in California suggest use of forests and heavily vegetated areas by foraging individuals (summarized by Pierson et al., 1999). In the Olema Valley of coastal California, Fellers and Pierson (2002) radio tracked 17 and directly observed 21 light-tagged Townsend's big-eared bats of both sexes and found that they flew around the perimeters of trees and foraged mostly along the edges of riparian woodlands rather than adjacent grazed grasslands. At Lava Beds National Monument 15 individuals of both sexes (females were non-reproductive or post-lactating) were radio tracked to determine foraging patterns (Pierson and Fellers, 1998). Three of four males moved less than females, ranging within 3.0 kilometers of day roosts, and showed repeated nightly patterns favoring mountain mahogany (*Cercocarpus* sp.) habitats; females moved more widely (up to 14.0

kilometers from roosts) and were triangulated to mountain mahogany, juniper, and ponderosa pine habitats with greater frequency than the abundant scrub habitats, although concentrated foraging was also observed in sparsely vegetated lava trenches where moths were visibly abundant (Pierson and Fellers, 1998). Radio-tagged bats foraged over areas that had been subject to a controlled burn at comparable frequencies as over unburned areas (Pierson and Fellers, 1998). On Santa Cruz Island in the California Channel Islands, six radio-tagged Townsend's big-eared bats moved at about 30 kilometers per hour during nightly foraging, with some moving over four kilometers from the roost; foraging was concentrated along slopes with native vegetation including coastal sage scrub oak (*Quercus dumosa*), coast live oak (*Quercus agrifolia*), ironwood (*Lyonothamnus floribundus*), and hollyleaf cherry (*Prunus ilicifolia*) rather than areas with non-native vegetation (Brown et al., 1994). The foraging period lasted about three hours, followed by a night-roosting period in shallow caves in the foraging area, and a short foraging period prior to returning to the day roost in a building (Brown et al., 1994).

Studies of all U.S. subspecies of Townsend's big-eared bats suggest insects of the order Lepidoptera are the primary component of the diet, particularly noctuid and sphingid moths, but other prey groups are also taken, including coleopterans, dipterans, and hemipterans, (Ross, 1964, 1967; Whitaker et al., 1977, 1981; Dalton et al., 1986; Sample and Whitmore, 1993; Burford and Lacki, 1998; Leslie and Clark, 2002; Ober and Hayes, 2008; Van Den Bussche et al., 2016). Dietary analysis of stomach contents of Townsend's big-eared bats from northwestern Colorado indicated that trichopterans were the dominant dietary component, followed by lepidopterans, dipterans, and hymenopterans at proportionally equal frequencies (Armstrong et al., 1994). Based on analysis of digestive-tract contents of individuals sampled from New Mexico and Arizona, Ross (1964, 1967) suggested that most lepidopterans taken were small, in the three to 10 millimeters length range. In West Virginia and eastern Kentucky, many of the moths used as prey by the Virginia big-eared bat had forest trees as host species rather than grasses or herbaceous vegetation, and several of the prey species were considered forest pests (Sample and Whitmore, 1993; Burford and Lacki 1998). It is uncertain if this also is true for the more western subspecies.

ROOSTING HABITS.— Townsend's big-eared bats are cave dwellers that typically roost suspended from open cave ceilings or high walls rather than retreating into fissures and crevices within caves (Pearson et al., 1952). They are also found in abandoned mine tunnels (this has been known for well over a century; for example, Grinnell and Swarth, 1913), rock shelters and under boulders and crevices on cliffs near the ground (for example, Ives, 2015), occasionally in old buildings (for example, Bailey, 1936; Dalquest, 1947a; Swenson and Shanks, 1979; Brown et al., 1994) and basal hollows of trees (Fellers and Pierson, 2002; Mazurek, 2004). It has been reported that in California old mines provide an important proportion of maternity and hibernation sites (Altenbach and Pierson, 1995; Pierson et al., 1999), and in Colorado most known roosting sites are also in old mines (Belwood and Waugh, 1991). In a 1996–1998 survey that included winter, spring, summer, and autumn seasons, 676 abandoned mines and 39 caves in northern Utah were searched for Townsend's big-eared bats (Sherwin et al., 2000). These bats were found in a higher proportion of available caves in comparison to mines, and none were found roosting in 105 bridges that were also examined. The lack of known long-distance seasonal movements away from roosts (see below) may limit local populations of Townsend's big-eared bats to areas with cavernous geological substrates (for example, karst or lava tubes) or to mining districts, unless roosting behavior patterns in alternate roosting structures have become established. Use of specific roosts is dependent on the favorability of their thermal regimes and the likelihood of disturbance.

Winter Roosts: In winter, Townsend's big-eared bats hibernate in caves and mines, both singly and in small clusters of mixed sexes, with the numbers counted within any single hibernaculum usually not exceeding the hundreds. For example, numbers of hibernating bats observed per cave ranged from 0 to 274 in counts at six caves surveyed every other year from 2004 to 2013 on Mount St. Helens in Washington (Wainwright and Reynolds, 2013). Observations in abandoned mines in western and central Nevada recorded numerous mines each with very small numbers of hibernating individuals (Alcorn, 1944; Szewczak et al., 1998; Kuenzi et al., 1999). Seven out of 260 mines examined by Szewczak et al. (1998) had 19–80 bats each, with the remainder having none to a few individuals (Szewczak et al., 1998). Observations in Utah were similar, with one or two bats per site when present and a maximum of 13 recorded during winter searches of over 500 mines and caves (Twente, 1960). Townsend's big-eared bats were the most common species noted during cave and mine surveys in Montana (Hendricks, 2012). A survey in the Black Hills of South Dakota during 1969–1970 reported Townsend's big-eared bats hibernating in total numbers ranging from one to about 1,000 in 15 caves and mines at elevations from 1,158 to 1,917 m; ambient temperatures at a subset of these caves and mines varied from three to 12ºC, with a mean of 6.1ºC (Martin and Hawks, 1972). Counts over the past half century at Jewel Cave National Monument in the Black Hills consistently number ≥ 600 (Choate and Anderson, 1997; records on file at Jewel Cave National Monument).

The largest number of hibernating Townsend's big-eared bats counted at a single cave at Lava Beds National Monument in northern California, an area with protections and an increasing population, was 699 bats in 2004 (Weller et al., 2014). Several limestone caves at 800–1,200 meters elevation in northern California had solitary individuals and groups of three to 50 Townsend's big-eared bats during winter surveys (Graham, 1966; Marcot, 1984). About 185 bats were documented using nine of 31 lava tube caves examined in Idaho (Genter, 1986). A winter colony of 500–600 individuals has been consistently observed in a cave in the mountains of Colorado since the late 1950's (Siemers and Neubaum, 2015). The largest number observed in hibernation in the western United States was 10,000 in a mineshaft in New Mexico discovered by J.S. Altenbach in 1992 (Pierson and Rainey, 1998a). This species also hibernates in irrigation tunnels in Colorado (Armstrong et al., 1994). In addition to use of inactive mines, about 190–200 were observed hibernating in clusters of two to 20 individuals in a working gold mine in southwestern Colorado (Armstrong et al., 1994). Hibernacula can include several other species of bats.

Factors associated with use of abandoned mines as hibernacula for Townsend's big-eared bats have been investigated in southwestern Colorado (Ingersoll et al., 2010; Hayes et al., 2011). Hayes et al. (2011) found 99 bats hibernating at 38 out of the 133 abandoned mines examined (mean 2.6, range one to eight bats per occupied mine, with nearly all bats roosting solitarily). Ingersoll et al. (2010) reported a mean of 2.3 hibernating bats at 61 of 158 mines examined. Temperatures near hibernating bats averaged 4ºC (range -2.6–9.0ºC) in the study by Hayes et al. (2011). In one analysis, the mine site variables thought to be most important included temperature at the mine portal and number of openings, with other possibly important factors including depth; the most important factor believed to influence hibernacula use at a landscape scale was mean annual ambient temperature (Hayes et al., 2011). As in other studies of caves and mines, number of openings was thought to be an important variable because the increased air exchange allows bats to take advantage of a greater range of internal temperatures. Ingersoll et al. (2010) also found that increased structural complexity of abandoned mines was an important variable in their use as hibernacula by this species.

In a study in Idaho, habitat characteristics associated with use of lava tube caves as hibernacula by Townsend's big-eared bats were investigated by Gillies et al. (2014). Twenty-four habitat variables (including indices of human visitation) were measured at different scales. Compared to unoccupied caves, caves used as hibernacula were farther from ephemeral water sources. Factors that may have been important but lacked statistical significance ($\alpha = 0.05$) in univariate analysis included observations suggesting that occupied caves seemed longer, had higher ceilings, more constrictions, and higher levels of humidity. A multivariate discriminant analysis indicated that three factors were of importance for occupancy: increased distance from ephemeral water, cave height, and presence of collapses or constrictions. The likely biological reasons for these findings were not entirely clear (Gillies et al., 2014).

Townsend's big-eared bats may arouse and change positions within or among hibernacula during winter (Twente, 1955a; Kunz and Martin, 1982; Genter, 1986), and winter-feeding activity may occur (Pearson et al., 1952; Ingersoll et al., 2010). Three individuals captured during winter over watering sites in New Mexico, however, did not show signs of active feeding (Geluso, 2007). This species tends to select the colder parts of caves and mines for hibernation rather than the warmest chambers and may be found close to entrances or in other well-ventilated areas, but they will shift to deeper, more thermally stable areas during winter extremes (Kunz and Martin, 1982 and references therein). Lowest mean monthly temperatures at Kansas and Oklahoma roost sites ranged 4.6 to 5.5ºC, and these sites had strong to moderate airflow (Humphrey and Kunz, 1976). In Idaho, these bats hibernated in lava-tube caves, but not those with extensive subfreezing temperatures, with nine of 31 caves surveyed harboring from seven to 132 bats (Genter 1986). In California, hibernating temperatures at 33 sites averaged 7.1ºC (Pierson and Rainey, 1998a). Interim roosts may be used by females subsequent to hibernation but prior to formation of maternity colonies (Dobkin et al., 1995).

Warm Season Roosts in Caves and Mines: Day roosts for 100 bachelor groups and 12 maternity colonies of Townsend's big-eared bats were found in the mines and caves surveyed in Utah by Sherwin et al. (2000). Maternity colonies numbered up to 550 mature females, averaging 129 females per site (Sherwin et al., 2000). They were more likely to be found in caves or mines with single openings, smaller entrances, and little evidence of human disturbance. Maternity groups, however, favored caves over mines and tended to use complex sites with multiple openings and multiple internal levels with large internal dimensions; unfortunately these sites also showed signs of frequent human disturbance (Sherwin et al., 2000). A subsequent study of 1,345 mines and 47 caves surveyed at multiple times of the year in 6 study regions of Utah and Nevada had objectives of determining patterns of roost fidelity and use in relation to habitat characteristics (Sherwin et al., 2003). Townsend's big-eared bat use was found at 590 sites, with used caves and mines mainly located below 2,600 meters in elevation; other patterns of habitat associations varied by study region (Sherwin et al., 2003). Most caves were used year-round, but mine use varied seasonally, with evidence of much discontinuous use of mines within seasons due to movement between roosts, particularly in small colonies within warm seasons; even maternity colonies moved to an average of three roosts in mines (range one to 9) every zero to seven days within a summer but following predictable patterns, whereas high fidelity was shown to caves (Sherwin et al., 2003). This study showed that intensive fieldwork and careful analysis is required for regional management of abandoned mine habitats for Townsend's big-eared bats.

Humphrey and Kunz (1976) recognized four seasonal roosting phases of Townsend's big-eared bats in Kansas and Oklahoma: nursery or maternity groups, summer males, winter populations, and occasional transient groups. In that region, females form maternity colonies of 17–40 adults in summer and cluster in warmest reaches of caves, mines, and buildings. (Early authors suggested that adult females do not cluster in maternity roosts [for example, Howell, 1920a], but many others have since reported such clusters, which are essential to bioenergetics of reproduction). Females in maternity groups in Oklahoma caves occupied warm ceiling domes seven to 12 meters wide. Maternity groups formed round, densely packed clusters of 35 to 81 adults and young in order to maintain high body temperatures to facilitate growth and development of young. No other species roosted nearby (Humphrey and Kunz, 1976). Females were usually not torpid and were alert (except during cold spells) in maternity colonies, which dispersed in late summer. One of the largest non-winter aggregations reported in recent times was observed in September 1976, when "several hundreds" were reported from "Stanton Cave" [Stanton's Cave] in Grand Canyon (Suttkus et al., 1978:4). More than 1,000 individuals have been counted emerging from a maternity colony in an abandoned mine that taps into a geothermally heated cave in the mountains of western Colorado (Siemers and Neubaum, 2015).

Males were detected in surveys of mine tunnels in the Huachuca Mountains of southeastern Arizona during 1949–1951, where nearly every tunnel had Townsend's big-eared bats, often in the same roosts used by Mexican long-tongued bats (Hoffmeister and Goodpaster, 1954). Males remain solitary or roost in very small groups, with an occasional few found among females in maternity colonies or in different parts of the same cave or mine (Howell, 1920a; Humphrey and Kunz, 1976; Kunz and Martin, 1982 and references therein; Pierson et al., 1991; Sherwin et al., 2000). Bachelor roosts (containing only males and non-reproductive females) were found in about 25% of 715 caves and mines surveyed in Utah, each housing one to seven individuals (Sherwin et al., 2000). During summer, males often roost solitarily near entrances of caves, mines, and buildings, but small numbers can sometimes be found scattered elsewhere in the same roost (Humphrey and Kunz, 1976, Sherwin et al., 2000). Males in some mines can show fairly deep daily torpor during summer, particularly at mid-elevations in mountainous region (Grinnell and Swarth, 1913; Dalquest, 1947a).

Warm Season Roosts in Structures other than Caves and Mines: Although caves and abandoned mines are the most important roosting habitat for this species, they also have been documented using buildings, tree hollows (Fellers and Pierson, 2002; Mazurek, 2004), and spaces under boulders or in crevices in rock outcroppings. The latter was reported in ponderosa pine forests in northwestern Arizona (Herder and Jackson, 2000), and two adult males radio tracked to roosts for six to 15 days in the Jemez Mountains of New Mexico roosted solitarily in three separate, small rock crevices low on cliff walls (Bogan et al., 1998). In western Nevada, radio-tracked males and non-reproductive females frequently roosted solitarily in such crevices rather than nearby caves or mines, switching roosts daily (Ives, 2015).

Townsend's big-eared bats will roost in buildings throughout their range in the western United States. As examples, Cryan (1997) reported a maternity colony of about 40 females and young in the attic of an abandoned building in South Dakota; a maternity colony of 300 adult females was observed in an attic in eastern Oregon (Betts, 2010); a lone roosting female was found in an attic in Utah (Hardy, 1941); and a colony of 12 was observed during September in an abandoned farm building in northeastern Montana (Swenson and Shanks, 1979). In California, Dalquest (1947a) described a maternity colony of about 75 bats, most in a tight cluster, in the attic of a mission in Alameda County, a smaller maternity colony in an attic of a winery in Napa County, and multiple buildings housing isolated males. A maternity colony of 130–145 adults and volant young used a two story adobe ranch building on Santa Cruz Island, California during summer 1992, where a larger colony of about 300 was known from the attic of an old building on the island during the 1930s and 1940s (von Bloeker, 1967; Brown et al., 1994). The only known roosting sites of this species in coastal areas of California are in old buildings, a bridge, and large basal hollows in trees (Gellman and Zielinski, 1996; Pierson et al., 1999; Fellers and Pierson, 2002; Mazurek, 2004). Bridges were found to house diurnal roosts of these bats in the central Sierra Nevada of California (Pierson et al., 2001). In western Colorado, a maternity colony of Townsend's big-eared bats numbering as many as 90 individuals has been found roosting during warmer months inside a hollow section of raised road and bridge on a busy interstate freeway (Siemers and Neubaum, 2015). A reproductive female caught over an ephemeral pool in the canyons of Colorado National Monument was tracked to a house in an adjacent suburb in the city of Grand Junction, Colorado (Neubaum, 2017).

Movements From and Among Roosts: Townsend's big-eared bats are not known to be long-distance migrants. In an approximately five-year study involving 1,500 banded individuals in California, almost all banded bats were found at the same place or within about 2.4 kilometers of the site where first banded in previous years; the maximum distance moved by a banded individual was 32 kilometers in a male (Pearson et al., 1952). In Kansas and Oklahoma, 194 recaptures of 827 banded bats over a seven- to 11-year study also showed that the species is fairly sedentary: only 16 bats were recovered at sites other than the place of banding, and 86% of these made movements of less than 1.6 kilometers; only two moved to roosts greater than eight kilometers apart (Humphrey and Kunz, 1976). Distances between maternity roosts and hibernacula of three bats ranged about three to 40 kilometers (Humphrey and Kunz, 1976). Three radio-tagged big-eared bats in central Oregon dispersed 11–24 kilometers from the hibernacula in spring (Dobkin et al., 1995). However, three females banded during winter in the Black Hills of South Dakota were subsequently recovered at three different localities during summer, all of which were more than 50 kilometers away from the hibernaculum (Cryan, 1997). Townsend's big-eared bats marked with passive integrated transponder (PIT) tags at a maternity colony in the mountains of western Colorado were subsequently found in a large hibernacula in a cave approximately 50 kilometers from the maternity site (Siemers and Neubaum, 2015).

Switching of roost sites by maternity colonies can occur, sometimes based on temperature preferenda at different phases of reproduction and development (Pierson et al., 1999, Sherwin et al., 2000). Fellers and Pierson (2002) noted the presence of adult males in a roost comprised mostly of females during mid-September. In northern Utah, autumn and spring use of mines and caves showed high variability, with frequent movements among different sites (Sherwin et al., 2000). This species uses abandoned mines as autumn swarming sites, behavior that appears to be critical for mating and maintaining genetic diversity (Ingersoll et al., 2010; Siemers and Neubaum, 2015). Some abandoned mines used for swarming are also used as hibernacula, whereas others are used exclusively for swarming; temperatures at swarming sites were cool enough for efficient energy assimilation, but warm enough to facilitate frequent arousals. At mines used for hibernacula in Colorado, the numbers of swarming individuals were positively correlated with numbers that use the same sites as hibernacula (Ingersoll et al., 2010).

Night Roosts: Townsend's big-eared bats utilize night roosts in caves, mines, small rock shelters, under bridges, buildings, or other sheltered sites. Some night-roosting bats may not return to the diurnal roosts until shortly before dawn (Pearson et al., 1952; Pierson et al., 1996b), although activity patterns vary seasonally and with stage of reproduction (Pierson et al., 1999). Night roosts are sometimes shared with other species. In Colorado, captures at entrances suggest possible use of caves as night roosts by small numbers of individuals (one to six) at each cave (Siemers, 2002). Similar findings were reported at Oregon Caves National Monument (Albright, 1959). Townsend's big-eared bat is well known to night-roost in buildings (for example, Dalquest and Ramage, 1946). Bridges are used by night-roosting individuals, as documented in the central Sierra Nevada of California and the Willamette Valley of Oregon (Perlmeter, 1996; Pierson et al., 2001). Use of large basal hollows in trees as roosts in California apparently also includes use as night roosts (Gellman and Zielinski, 1996; Fellers and Pierson, 2002).

Population Ecology.— Litter Size, Natality, and Female Reproduction: A single offspring at birth is well-documented throughout the range of Townsend's big-eared bat in western

North America. One embryo was reported in each of three females taken in California (Grinnell and Swarth, 1913; Grinnell, 1918), Howell (1920a:174) described "about a hundred females, each with a naked young" in a maternity colony in an old mine along the lower Colorado River in California, and only single young were reported during dissection of about 260 reproductive females in an in-depth northern California study (Pearson et al., 1952). Single embryos were found in three females from the vicinity of Carlsbad Caverns National Park, New Mexico (Geluso and Geluso, 2004), in one female from the Black Hills of South Dakota (Turner and Jones, 1968), in one female from Big Bend National Park, Texas (Easterla, 1973), in two females from the Chiricahua Mountains in southeastern Arizona (Cockrum and Ordway, 1959), and in two females from the Grand Canyon in northern Arizona (Ruffner et al., 1978). Cockrum (1955) summarized over 30 other cases from throughout the western states of females with single embryos, as well as additional cases of females with accompanying single young. However, Hall (1946) noted nine females with single embryos and one female with twins near Fallon, Nevada.

The proportion of females in an area that are reproductive is variable, with estimates likely biased high by captures at maternity colonies. Easterla (1973) reported 99% of 76 females captured at maternity roosts and over water as reproductive in his studies at Big Bend National Park in Texas, and Fenton (1969) reported 100% reproductive in a sample of 37 bats captured at a presumed maternity colony in a nearby region of Texas. Thirty-nine of 40 adult females (97%) sampled at maternity roosts in western Oklahoma in 1968 were reproductive (Humphrey and Kunz, 1976), one of two females taken in Riverside Mountain in the lower Colorado Desert of California was reproductive (Grinnell, 1914), and 94% of 470 females examined at maternity roosts early in pregnancy in central California during 1947–1950 were reproductive (authors cautioned this proportion might decrease as embryos were resorbed later, and that some non-reproductive females are likely not present in maternity roosts; Pearson et al., 1952). All of eight females (100%) taken primarily at roosts in the Mogollon Mountains of southwest New Mexico and adjacent Arizona during June and July in 1960 to 1961 were reproductive (C. Jones, 1964). In South Dakota, 91% of 22 females captured at maternity roosts were reproductive (Turner and Jones, 1968). In Colorado, all of 21 captured in a mine in Chafee County from mid-June to late July were reproductive (capture method unspecified), and four of 6 examined at a mine in La Plata County during mid-June were pregnant (Freeman and Adams, 1992 cited in Armstrong et al., 1994). Four of four females taken over water at Morefield Canyon at Mesa Verde National Park in southwestern Colorado during early August were lactating (Chung-MacCoubrey and Bogan, 2003). All of 19 females from maternity roosts near Pyramid Lake in Nevada were reproductive in 1924 (Hall, 1946), whereas 64% of 14 females sampled over water in west-central Nevada in 1994 were found to be reproductive (Kuenzi et al., 1999). Biases towards higher assumed natality rates from sampling at maternity colonies is also indicated by the known roosting of non-reproductive females solitarily or in small groups at scattered locations other than maternity roost sites (for example, Pierson et al., 1999; Sherwin et al., 2000, 2003).

Not all female Townsend's big-eared bats breed in their first year of life, and young males probably do not mate at all during their first year (Pearson et al., 1952). Nine of 26 non-reproductive females in an intensive California study were yearlings, and nine of 34 (26%) of the known-age one-year-old females in that study were non-reproductive (Pearson et al., 1952). We are unaware of any other published literature with quantitative data concerning age at first reproduction or inter-birth intervals. Mating may occur in hibernation throughout the winter in multiple copulations, with subsequent sperm storage until ovulation and fertilization take place in spring (Pearson et al., 1952). Sex ratio at birth is 1:1 (Pearson et al., 1952).

Survival: Pearson et al. (1952) indirectly estimated survival of females in California by recording returns of yearling and adult females to a maternity site each year for three years (thus emigration must be assumed to be negligible). Adult return rates were 70–80%, whereas yearlings returned at a rate of roughly 40 to 50%. Stable colony sizes were considered likely if recruitment of young was 50% the first year and survival of adults was 80% annually (Pearson et al., 1952). Pre-weaning mortality in this species is thought to be about four to five percent (Pearson et al., 1952; Humphrey and Kunz, 1976).

Survival analyses using modern analytical methods were carried out retrospectively on banded Townsend's big-eared bats using three cave systems as hibernacula in Washington (Ellison, 2010). Banding took place during 1964–1975 with 1,123 individuals banded and recaptures continuing until 1980. Annual apparent survival estimates varied from 54% to 76% using model-averaging techniques, survival tended to be lower in males than in females, and estimates of capture probability ranged widely. The cave system with the largest sample size showed an upward trend in survival with time through 1980, but it had a negative trend in capture probabilities (Ellison, 2010). Basic survival estimates were mostly lower than those calculated for other species of temperate zone bats with similar demographic traits that had stable or growing populations (O'Shea et al., 2011c). Banding at this site was known to cause injuries to this species, and banders thought that the associated disturbances may have had negative impacts (perhaps including permanent emigration) that were reflected in the estimates (Ellison, 2010). Newer efforts to conduct survival analysis on this species are underway in western Colorado, where over 600 individuals have been marked with PIT tags at a summer roost equipped with devices that automate the recording of bat presence and activity (Siemers and Neubaum, 2015).

Townsend's big-eared bats banded in California provided a published maximum longevity record for this species of 16.4 years (Paradiso and Greenhall 1967).

Mortality Factors: Known mortality factors include incidental records of predation by gopher snakes (*Pituophis melanoleucus*) in caves (Galen and Bonn, 1979), by black rats (*Rattus rattus*) in buildings (Fellers, 2000), and by domestic cats at entrances to gated caves occupied by Townsend's and Virginia big-eared bats (Bagley and Jacobs, 1984; Jewel Cave National Monument, written commun.). Townsend's big-eared bats are subject to deaths from rabies (for example, Constantine, 1979, 1988; Mondul et al., 2003; Blanton et al., 2007). Ectoparasites and endoparasites have been described but not linked with mortality (for example, Jameson, 1959; Rausch, 1975, Reisen et al., 1976; Ritzi et al., 2001; Sastre et al., 2016; for summary of earlier work see: Sparks and Choate, 2000; Whitaker and Wilson, 1974). In their intensive study of this bat in California where over 1,500 individuals were banded and subsequently searched for over several years, Pearson et al. (1952) suggested that disease and predation were unlikely to be factors limiting population size, but that the number of suitable winter roosting sites and summer roosts with adequate feeding areas were critical.

Chemical residue surveys for contaminants have been carried out in guano and carcasses of the endangered subspecies of Townsend's big-eared bats (Martin, 1992; Ryan et al., 1992), but deaths due to chemical contaminants are unknown. A colony of these bats was likely eliminated by mortality due to exposure to cyanide in drinking water from a gold-mining operation in California (Brown and Berry, 1991; Clark and Hothem, 1991). Potential absorption of radon was estimated for this species using caves and abandoned uranium mines at 7 micrograms per year during winter and 139 micrograms per year during summer, but the health effects of such exposure remain unknown (Schmidt, 2014).

Blood samples from three individuals sampled from a cave in western Oklahoma during February of 2011 were negative for antibodies to *Pseudogymnoascus destructans*, the fungal agent of white-nose syndrome (Brennan et al., 2015). Although white-nose syndrome has been documented in species of *Myotis* inhabiting several caves also used by apparently unaffected eastern subspecies of Townsend's big-eared bat (Johnson et al., 2012b), it was not until 2017 that an individual of this species in Texas tested positive for *P. destructans* (no mortality or clinical signs of disease were observed; Texas Parks and Wildlife, 2017). Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with anti-fungal properties on wings of these bats and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America.

A hibernaculum in New Mexico that housed more than 10,000 Townsend's big-eared bats in 1992 had been set afire by vandals the same winter, with hundreds of carcasses evident and thousands presumed dead (Pierson and Rainey, 1998a; Pierson et al., 1999).

Population Trend: There has been considerable interest in the population status of the western subspecies of Townsend's big-eared bat over the past 25 years, resulting in a number of efforts to document colony sizes at hibernacula and maternity roosts (Ellison et al., 2003). One recent analysis has shown that some of these surveys can be useful for inference about local population trends (Weller et al., 2014; see below). Compilations of other data sets in the past, however, showed limitations to analysis of independently documented survey data. Ellison et al. (2003) showed that only 15 hibernacula and six summer colonies of the western subspecies that they had obtained included four or more separate years of records available for analyses. Statistically significant nonparametric trends were undetectable for 12 of the 15 hibernacula, with one of the remaining three increasing and two declining; similarly, trends were not detectable in five of six summer colonies, with one showing a significant decline (Ellison et al., 2003). The population in the hibernaculum at Jewel Cave National Monument declined from about 3,750 in 1959 to 853 in winter 2000 (Ellison et al., 2003), with a marked drop from 1959 to 1967 when much banding of bats was conducted (Choate and Anderson, 1997). Banding injuries and disturbance of several species of bats probably contributed significantly to increased mortality during the era of large-scale bat banding activities (for reviews see O'Shea et al., 2004; Ellison, 2008). Prendergast et al. (2010) analyzed trends in counts of Townsend's big-eared bats made at 10 hibernacula in gypsum caves in Kansas and Oklahoma, also using a non-parametric statistical approach. Counts were made intermittently during 1965–2004, ranging from 0 to 235 individuals over the course of five to 11 annual surveys. No trend was detectable in counts at eight hibernacula, with one colony showing a decrease and one showing an increase (Prendergast et al., 2010).

Although limitations to most trend analyses were apparent from independently acquired *post hoc* count data sets for Townsend's big-eared bats in the western U.S., Weller et al. (2014) provided a good recent example of how such data nonetheless can be usefully applied to make inferences about local population trends. They compiled winter count data from 52 of 97 caves surveyed over the period 1991–2012 at Lava Beds National Monument in northern California. They used log-linear models following a negative binomial distribution to estimate slopes of trend lines over time and to predict future counts. Seventeen of 22 (77%) caves that had four or more years of count data showed positive trends, with counts in these more-frequently surveyed caves having an annual growth rate of about 4% (Weller et al., 2014). Combined estimated counts at all caves increased from 834 bats in 1991 to 1,427 in 2012, with an estimated positive annual growth rate of 1.8% during the period. The positive growth rates coincided with the implementation of more restrictive human visitation regulations (Weller et al., 2014). However, as Weller et al. (2014) point out, inferences apply only to their sample and overall trends at the approximately 750 caves at Lava Beds National Monument remain unknown.

Although there are few similar statistical analyses of trends in population sizes, most other available information on changes in populations of the subspecies *C. townsendii townsendii* or

C. townsendii pallescens documents declines. Surveys were conducted in California during the late 1980s and early 1990s that emphasized comparisons with historically occupied sites (based on records from the 1940s to 1960s). This work indicated that over an approximately 40-year period there was a 52% loss in the number of maternity colonies (24 of 46), a 55% decline in total numbers of adult females (from 3,004 to 1,365 at 18 maternity sites), a 44% decline in the number of available roosts, and a 32% decrease in average size of remaining colonies (Pierson and Rainey, 1998a). Bats in the area of a maternity site numbering 140 and a hibernacula of 65 studied by Pearson et al. (1952) in 1949–50 in northern California had declined to about 70 and 26, respectively, in 1987–88; a maternity colony numbering about 200 bats in the 1960's in a separate area in the same region appeared to be reduced to about 150 in 1987 (Pierson et al., 1991). Overall, four hibernation sites in California studied by Pearson et al. (1952) that housed a total of 470 bats held just 59 individuals in the late 1980s and early 1990s (Pierson and Rainey, 1998a). Numbers of hibernating bats at two sites in Lava Beds National Monument in California remained at about 30 between 1949 and 1988. In coastal California, only seven small colonies were known for *C. townsendii townsendii* in 1989, with just three actively protected (Pierson, 1989).

The survey report for California (Pierson and Rainey, 1998a) also summarized unpublished information and reports from investigations by others on the status of this species in some other western states. These other studies also document declines, albeit frequently anecdotal and subject to bias. Major declines were noted at sites in Oregon and Washington. Intensive surveys for maternity colonies over large areas in Nevada revealed only two sites with small groups. Four hibernacula in Idaho experienced a 60% decline since 1987. As noted above, a group of more than 10,000 hibernating in a mine in New Mexico was reduced by several thousand after vandals burned the site during winter (Pierson and Rainey, 1998a; Pierson et al., 1999). Subsequent gating at mine entrances at the complex of mines involved suggested that some recovery had occurred (Kretzmann, 2000). In Arizona, two historically known populations in caves had disappeared, and another with historical estimates of several hundred adult females dropped to less than 100 (Pierson and Rainey, 1998a). A mine in the Hualapai Mountains of Arizona that served as a hibernaculum for 1,500 bats in 1962 held about 100 bats in 1997–1998 (Brown and Berry, 1999). An increase in abundance between 1972 and 1997 at one site in Arizona occupied by a small colony of breeding females was reported by O'Shea and Vaughan (1999), who suggested that the 1997 numbers remained below those presumed present when mammalogists first visited the site in 1931. Mist-netting surveys over a small desert spring in southern Nevada found this species to be equally rare between two sampling periods separated by about 50 years (O'Farrell and Bradley, 1970; O'Shea et al., 2016b).

Population estimates for both subspecies considered species of concern are not available over the entire range. However, past estimates have been made in some areas which may be useful for trend comparisons in the future. A gross estimate of 11,000 *C. townsendii pallescens* over the southern Great Plains (Kansas, Oklahoma and Texas), thought likely to be biased upwards, was calculated by Humphrey and Kunz (1976) for the early 1970's. In Kansas, the population is centered in the south-central part of the state. A summer population of 300 to 500 was estimated by Twente (1955a) for south-central Kansas and adjacent areas in Oklahoma. The total number of adult females at 38 maternity colonies in California in the late 1980s-early 1990s was 4,250 (Pierson and Rainey, 1998a). Other unpublished information summarized by Pierson and Rainey (1998a) indicated that in 1990 about 2,700 adult females occurred at known sites in Oregon, and about 800 adult females occupied known sites in Washington. A large maternity colony was observed as a cluster of about 100 (90 taken in one attempt with a hand net) at a cave in eastern Washington in 1929 (Scheffer, 1930), and a maternity colony of about 200 was observed in an abandoned mine at about 1,300 meters in piñon-juniper habitat in Mohave County, northwestern Arizona during 1959 (Cockrum et al., 1996). Only a single maternity colony is now known from old mines along the Lower Colorado River in California, where colonies in other mines known historically have disappeared (Brown, 2013). One factor implicated in these losses along the river is suspected reductions in availability of insect prey associated with loss of native vegetation to agriculture and the concomitant intensive use of insecticides (Brown, 2013).

Additional detailed accounts on past status of numerous colonies of Townsend's big-eared bats are given in a state-by-state review conducted during the late 1990s (Pierson et al., 1999). Sizes of colonies known at the time were included, as were changes in use and counts in comparison with past results, and identification of likely causes for declines and present levels of protection. Most of the information supports the perception of serious declines in western populations of this species (Pierson et al., 1999). Sites identified in the report by Pierson et al. (1999) may be useful to re-visit to determine current status.

Population Genetics: Despite threats and evidence of past declines in local populations, genetic diversity is not dangerously low in *C. townsendii pallescens* nor in *C. townsendii townsendii* (Piaggio et al., 2009) perhaps with exceptions in some localized areas (Smith et al., 2008). However, Lack and Van Den Bussche (2009) tentatively concluded that the current population size inferred from genetic measures may be declining when compared to genetic estimates of past population growth over the recent evolutionary history of the species.

MANAGEMENT PRACTICES AND CONCERNS.— A detailed plan specifying threats to populations of Townsend's big-eared bats and management practices for their amelioration can be found in the conservation strategy prepared by Pierson et al. (1999). The strategy also includes recommendations for roost surveys, inventory and monitoring, protocols for evaluating use of abandoned mines as bat roosts, and examples of effective gate designs.

White-Nose Syndrome: Eastern subspecies of Townsend's big-eared bats (Virginia big-eared bat and Ozark big-eared bat) presumably have been exposed to the fungus that causes white-nose syndrome for several years after the epizootic reached their populations (Johnson et al., 2012b; Arkansas Game and Fish Commission, 2014). Antibodies to the fungal agent of white-nose syndrome were not detected in three individuals sampled during 2011 in western Oklahoma, consistent with an absence of reports of gross lesions or mortality in the region at the time (Brennan et al., 2015). Even after *P. destructans* was genetically detected on a western subspecies of Townsend's big-eared bats in Texas during 2017, clear indications of mortality or clinical signs of disease were not observed (Texas Parks and Wildlife, 2017). Fungal presence without obvious indications of deleterious disease effects have been noted in eastern subspecies of this bat for several years, and it has been suggested these bats have behavioral or physiological strategies for surviving white-nose syndrome (Johnson et al., 2012a; Coleman and Reichard, 2014). It remains unknown whether western subspecies of Townsend's big-eared bats will show similar lack of vulnerability to white-nose syndrome, but temperature conditions in some western hibernacula are thought to be suitable for fungal growth (Siemers and Neubaum, 2015).

Disturbance from Recreation and Vandalism at Roosts: This species has been characterized as intolerant of human activities and quick to abandon roosts that have been disturbed (Schmidly, 1991); females will move young to alternate roosts if disturbed (Pearson et al., 1952), but it is likely that disturbance may negatively affect reproductive success (Pierson and Rainey, 1998a). Pierson et al. (1991) noted that the species "is so sensitive to human disturbance that simple entry into a nursery roost can be enough to induce the colony to abandon a site." In California, only four of 54 maternity roosts known to exist in the late 1980s-early 1990s could be deemed secure, and none were thought to be capable of persisting into the long-term future without active protection measures; most hibernacula were also threatened by human disturbance, vandalism and recreation. These losses could be traced to human activities in all but two of 38 cases of roosts no longer used (Pierson and Rainey, 1998a). Vandalism, including shooting, bashing with clubs, and subjecting to fire, smoke, and fireworks has been reported (Pierson et al., 1999; Oliver, 2000). Graham (1966) noted that a cave housing a maternity colony in a California limestone cave had been permanently sealed closed. The illegal application of pesticides to destroy these bats in building roosts has also been documented in California (Pierson and Rainey, 1998a). Along the Colorado River, conversion of riparian and floodplain habitats to agricultural uses may have impacted populations of this and other species of bats through diminished quality of foraging habitat (Pierson and Rainey, 1998a; Brown, 2013). Remnant redwood forests may be important to these bats in coastal California (Fellers and Pierson, 2002).

Humphrey and Kunz (1976) also reported this species to be very sensitive to disturbance and to respond more negatively to banding than other bats, showing a high proportion of band-related injuries, particularly in females. They concluded that they should not be banded unless important new capture-recapture data are needed. Handling in summer maternity roosts also caused roost desertion, and a decline in nursery populations that did not recover in the following year was also apparent; population effects due to disturbance at hibernacula were not apparent. However, this species shows a high rate of weight loss in winter, suggesting that disturbance during winter could lead to increased fat depletion and winter mortality (Humphrey and Kunz, 1976). High susceptibility to disturbance has also been reported for the Virginia and Ozark big-eared bats (Currie, 2000a).

At Lava Beds National Monument in northern California, implementation of restrictions to human visitation in winter and during the maternity season coincided with overall positive annual growth trends in counts at 52 hibernacula (Weller et al., 2014). The study by Weller et al. (2014) also concluded that restricting counts at hibernacula to every other year (a recommended practice for many cave-hibernating bats including this species; Pierson et al., 1999; Kunz, 2003; Kunz et al., 2009) rather than annually would be unnecessary and would reduce the sensitivity of trend analyses and attribution of likely causes for observed change. Greatly increasing the number of caves surveyed (750 caves are present in the monument) and other adjustments to sampling protocols are expected to provide improvements to the scale of inference for future trend estimates (Weller et al., 2014).

Resource managers are often faced with difficult decisions in determining adequate levels of protection necessary for disturbance-sensitive species of bats. For example, in the western U.S. the potentially competing demands of recreational caving access, minimizing the risk of spreading the fungus that causes white-nose syndrome from human equipment, and the singular dependence of Townsend's big-eared bats on a limited number of caves have necessitated complicated management decisions (U.S. Forest Service, 2017). Unlike areas of eastern North America where multiple species of bats form large hibernation colonies (more than about 100 individuals) in caves during winter, Townsend's big-eared bat "…is the only species that can regularly be found hibernating in fair numbers in western caves and mines" (Barbour and Davis, 1969:165). Particular dependence of Townsend's big-eared bats on caves most likely to be used for human recreation in the western U.S. highlights the need to consider the particular needs of each bat species when developing management strategies. Using the case of Townsend's big-eared bats in Colorado as white-nose syndrome approaches, Neubaum et al. (2017) proposed criteria for prioritizing important bat roosts where management efforts could be focused. These criteria included a focus on roosts used during any time of year by gregarious species for reproduction, social interactions, or hibernation, as well as those that if negatively disturbed or lost could affect five percent or more of the management-relevant local population (Neubaum et al., 2017).

Although evidence of abandonment and limitation of roost use after disturbance is consistent across regions in this species, Townsend's big-eared bats are known to sometimes tolerate certain kinds of disturbance: for example, a maternity colony consistently forms each year inside a noisy highway structure in Colorado (Siemers and Neubaum, 2015). Levels of disturbance are variable, with those involving direct vandalism or killing obviously the most egregious. In contrast, some long-term winter surveys and carefully conducted capture and marking efforts at maternity colonies have not resulted in obvious indications of roost abandonment or avoidance by Townsend's big-eared bats (Siemers and Neubaum, 2015).

Managing and Gating of Mines and Caves: Abandoned mines are dangerous to humans. In the recent past, public and private land managers sealed or destroyed openings to likely thousands of abandoned mines in the interest of public safety; it is thought that these actions had a major negative impact on populations of Townsend's big-eared bats throughout their distribution (Pierson et al., 1999). During the 1990s resource managers expanded programs to determine the use of mines by bats and to secure the entrances of those discovered to be roosts with structures that exclude people but allow bats access. Recreational disturbance of caves and abandoned mines is another major factor implicated in declines in populations of this species, and visitor restriction through gating is the most obvious management action that can address this problem as well.

Townsend's big-eared bats are among several species of bats that have been shown to use caves and mines with entrances secured by gates or in some cases cable-netting (for example, Pierson and Rainey, 1998a; Currie, 2000a; Navo et al., 2000; Sherwin et al., 2002). Spacing of bars of gates placed at entrances of old mines or caves used as roosts by this species such that openings are at least 15 centimeters high and 50 centimeters wide has been recommended; these dimensions maximize chances of acceptance by bats while maintaining goals of minimizing intrusions (Pierson et al., 1991; Navo, 2001; Sherwin et al., 2009). Townsend's big-eared bats have accepted alternative, gated roost sites in old mines in cases where previously used mines nearby had to be closed (Pierson, 1989; Enderlin, 2000); increased use of roosts by these bats subsequent to installation of protective gates also has been documented (Pierson and Rainey, 1998a). When closures of mines are necessary, such activities should be carried out at times when bats will not be entombed within them. The State of Colorado has a productive program and well-developed protocols aimed at determining use of inactive mines by bats, and these protocols have a strong focus on conservation of this species (Navo et al., 2000; Navo 2001). Over 300 inactive mines used by this species have been fitted with bat-compatible closures in Colorado (Annear, 2000). The National Park Service has utilized bat-compatible closure methods at abandoned mines used by this species at multiple sites around the U.S. (Burghardt, 2000).

Kretzmann (2002) described gate designs that have been used for protection of Townsend's big-eared bats at abandoned mines in New Mexico. Dozens of mines have been protected with gates or cable-netting in New Mexico with positive results (Pierson et al., 1999). Sherwin et al. (2002) review complexities in the use of gated mines by bats, and suggested that culvert/gate combinations and other designs can be effective and readily accepted by these bats. However, gating of entrances to occupied abandoned mines can affect behavior, especially soon after gates are installed. Diamond and Diamond (2014) reported higher rates of circling behavior in maternity colonies (averaging 84 to 112 individuals) during morning returns to gated mines in Utah, particularly at newly gated mines. They also documented greater crowding at emergence time, and more collisions with gates (presumably most collisions involving newly volant young) with the latter potentially increasing susceptibility to ground predators (Diamond and Diamond, 2014). Nonetheless, study authors suggest that these negative behavioral effects are likely outweighed by the positive effects of enhanced roost protection. In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that Townsend's big-eared bats continued using gated mines over the long-term, tolerated various gate designs, and that the landscape location and structural complexity of a mine were better than gate characteristics as predictors of whether this species would continue using a site after gating.

A study of 1,345 mines and 47 caves surveyed at multiple times of the year in six regions of Utah and Nevada (Sherwin et al., 2003; see above) showed that intensive field work and careful analysis are required for comprehensive regional management of abandoned mines as roosting habitat for Townsend's big-eared bats. Use of such roosts can follow complex seasonal patterns, and sites that are used by this species can be missed without such thorough studies, which unfortunately are seldom possible.

Resurgence of Mining by Modern Methods: A major conservation issue for Townsend's big-eared bats has arisen in historic mining districts, where renewed mining operations using modern techniques have resulted in complete removal of otherwise suitable abandoned mines; the largest then-known mine-roosting hibernating colony of Townsend's big-eared bat in California (166 bats) was destroyed by renewed mining in the 1980s (Pierson and Rainey, 1998a). These extensive mining operations have other consequences for bat populations, as pointed out by Clark (1991), Brown et al. (1993a,b), and Brown and Berry (1991). Old mine openings can be destroyed, surrounding landscapes altered, and water tables reduced by removal of water for mining and extraction processes, with resultant elimination of natural drinking sources in streambeds and loss of riparian vegetation used for foraging by some bats (Brown et al., 1993a,b; Brown and Berry, 1991). Mitigation of loss of roosts in historic mining districts through experimental creation of artificial roosting habitat has taken place at the McLaughlin Mine in northern California, but its acceptance by this species at the time was not determined (Enderlin, 2000). In this case, large used tires from heavy equipment were placed side to side to form tunnels, radiating in four directions from a central concrete hub, then covered with waste rock, clay, and soil.

Euderma maculatum — Spotted bat (Family Vespertilionidae)

CONSERVATION STATUS.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. Bureau of Land Management (2009a, 2010a,b,c, 2011a,b, 2015a,b, 2017): Sensitive Species (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Utah, Wyoming state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G4, Apparently Secure.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need. California Department of Fish and Wildlife (2017): Special Animals List, Species of Special Concern. Colorado Parks and Wildlife (2015b): Species of Greatest Conservation Need, Tier I. Idaho Department of Fish and Game (2005): Species of Greatest Conservation Need. Montana Fish, Wildlife, and Parks (2005, 2015a,b): Species of Greatest Concern, Species of Greatest Conservation Need. Nevada Department of Wildlife (2013): Threatened Mammal. Nevada Department of Conservation and Natural Resources (2015a): Imperiled. New Mexico Department of Game and Fish (2006, 2012): State Threatened, Species of Greatest Conservation Need, Vulnerable. Oregon Department of Fish and Wildlife (2005, 2008): Sensitive Species, Vulnerable. Texas Parks and Wildlife (2012, 2015): Species of Greatest Conservation Need, State Threatened. Utah Division of Wildlife Resources (2015; Sutter et al., 2005): Species of Greatest Conservation Need. Washington Department of Fish and Wildlife (2015a,b): Species of Concern, Species of Greatest Conservation Need. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier III.

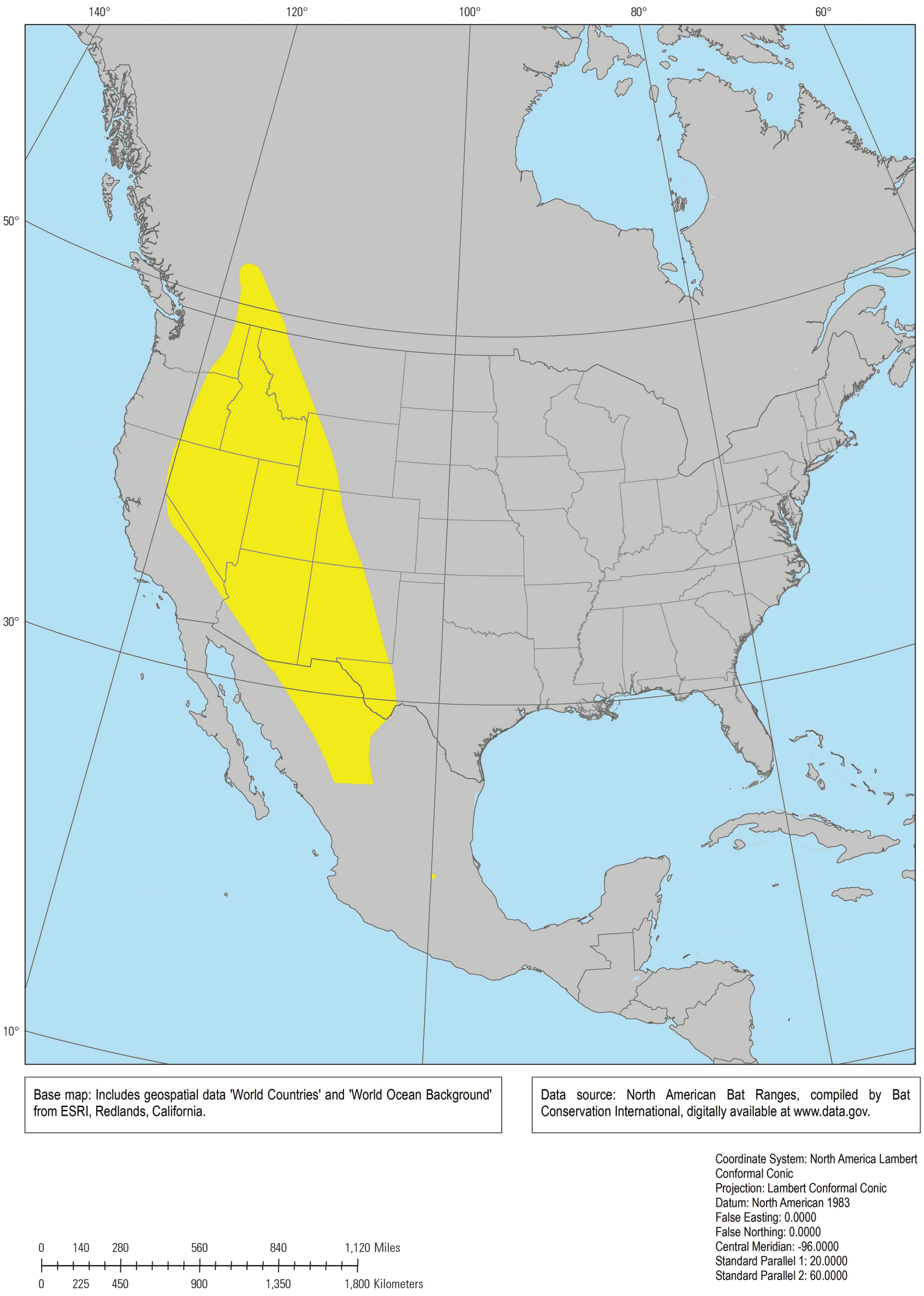
DESCRIPTION.— The spotted bat (Fig.11) has the most striking appearance of any species of bat in the United States. It has extremely large, pale ears (the largest of any North American bat) and three large white spots on a blackish-colored dorsum, one over each shoulder and one over the rump. The spotted bat is also a relatively large bat. Mean body mass of 36 males and 25 females from multiple locations in nine U.S. states, Canada and Mexico, averaged 15.3 grams in both sexes, but mean forearm length of females (52.1 ± 1.4 SD millimeters, range 49.7–55.0) was significantly larger than that of the males (50.1 ± 1.9 millimeters, range 43.9–53.1; (Best, 1988).

FIGURE 11. Spotted bat, *Euderma maculatum* (photo by J. Scott Altenbach).

DISTRIBUTION AND SYSTEMATICS.— Spotted bats occur in the western United States, Canada, and Mexico (Fig. 12). In the United States, they can be found in parts of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Utah, Washington, and Wyoming. Within these states they are very patchily distributed but are often found where cliffs that provide crevices for roosting are within flight distance (for example, Easterla, 1970, 1973; Poché, 1981; Fenton et al., 1987; Wai-Ping and Fenton, 1989; Storz, 1995; Perry et al., 1997; Pierson and Rainey, 1998b; Priday and Luce, 1999; Rodhouse et al., 2005). The scientific name of the spotted bat was first used in 1894 by Allen (1893). No subspecies are recognized. Watkins (1977) provided a taxonomic synonymy of past scientific names applied to the spotted bat. The generic name *Euderma* is a combination of two Latin words meaning “good” or “beautiful” and “skin”, and the specific epithet stems from the Latin word meaning “spotted”. Other English common names include pinto bat and black-and-white pinto bat; a Spanish common name is murciélago pinto.

HABITATS AND RELATIVE ABUNDANCE.— Spotted bats have been captured in many western U.S. habitat types at elevations ranging from 104 to 3,230 meters (Reynolds, 1981; Pierson and Rainey, 1998b). Dominant vegetation communities at capture sites include Mojave, Chihuahuan, and Sonoran deserts, Great Basin sagebrush, piñon-juniper woodlands, oak savannas, ponderosa pine, mixed conifer, and spruce-fir forests (for example, Benson, 1954; Easterla, 1965, 1970, 1973; Poché and Baillie, 1974; Bleich and Pauli, 1988; Berna, 1990; Geluso, 2000; Chambers et al., 2011). Although these bats are widespread, distributions are discontinuous and patchy, and the species can be relatively uncommon compared to many other species of bats. This bat was at one time so poorly known that C. Hart Merriam wrote in 1899 “that it was among the rarest mammals in the world” (Vorhies, 1935:225).

Fenton et al. (1987) surveyed for both echolocation and audible calls of these bats at 1,186 study sites grouped into 80 areas where the species had been previously reported or thought to occur. Sites were distributed from southern British Columbia to the U.S.-Mexico border. They



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 12. Approximate distribution of the spotted bat, *Euderma maculatum*. Species range is shown in yellow, but may extend farther south in Mexico.

found call-based evidence at 34 sites in 10 areas, supporting the hypothesis that spotted bats are uncommon compared to other species (Fenton et al., 1987). Many bat faunal surveys within the general distribution of the spotted bat fail to document their presence through captures (see below for examples), although they can be detected in more localized regions using acoustic survey techniques (for example, Navo et al., 1992; Storz, 1995; Kuenzi and Morrison, 1998; Pierson and Rainey, 1998b; Rodhouse et al., 2005).

Pacific Northwest and Northern Rocky Mountains: Published bat faunal surveys using mist nets over water in Oregon, Washington, and Idaho have not reported captures of spotted bats at the locations sampled (Whitaker et al., 1981; Thomas, 1988; Perlmeter, 1996; Baker and Lacki, 2004; Lacki et al., 2007), although their presence in these states is otherwise documented (Handley, 1959; Verts and Carraway, 1998; Hayes and Wiles, 2013). Spotted bats were the least abundant of nine species (two of 231 individuals) of bats captured over water in the Pryor Mountains of south-central Montana (Worthington, 1991).

One spotted bat was captured over water in the semi-arid Okanagan Valley of southern British Columbia, where the species ranked as least abundant of 12 species documented through capture of 958 individuals (Woodsworth, 1981). None were captured in an earlier survey in the same region, where an additional 351 bats of nine species were captured (Fenton et al., 1980).

California and Nevada: In the Sierra Nevada mountain range of California, the spotted bat ranked eleventh of 17 species (seven individuals among 390 bats) captured in mist nets at 19 sites during 1993–1999 (Pierson et al., 2001). None were captured among 1,398 individuals of 15 species taken in mist nets set over water during four summers in the upper Sacramento River area of northern California (Pierson et al., 1996b), and none were captured during mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats and yielded 403 bats of 10 species (Duff and Morrell, 2007).

In south-central Nevada, five of these bats were taken among 2,099 (0.2%) bats of 13 species captured in mist nets, ranking twelfth in relative abundance, and were netted only in Great Basin Desert habitat (Hall, 2000); three of these bats were captured among about 2,000 bats of 14 species netted over water in the White and Inyo Mountain ranges of Nevada and California (Szewczak et al., 1998). Spotted bats ranked tenth (three captured among 299 bats of 11 species) in mist-netting surveys over water in west-central Nevada in habitats categorized as desert shrub and piñon-juniper woodland zones (Kuenzi et al., 1999). In a comparative study of differential use of habitat types within riparian areas in the Mojave Desert of southern Nevada, acoustic activity of these bats over open riparian marsh was greater than any other species measured; they also were active over mesquite bosque but not riparian woodland or riparian shrubland (Williams et al., 2006).

Southwestern U.S.: ***Arizona***: Spotted bats were fourteenth in abundance (two captures among 3,458 individuals of 17 species) in a summary of mist-netting records over water in Mohave County of western Arizona (Cockrum et al., 1996), where authors remarked that their high maneuverability and habits of roosting in high cliffs reduce their susceptibility to capture in mist nets. They ranked ninth in abundance among 17 species of bats (18 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). They constituted 4% (47 captured) of about 1,175 individuals of multiple species sampled over water at multiple sites in extreme northern Arizona (Chambers et al., 2011). None were taken in surveys over water in ponderosa pine and mixed ponderosa pine-Gambel oak forest of north-central Arizona, where 15 other species and 1,673 individuals were captured (Morrell et al., 1999).

New Mexico: Spotted bats ranked seventeenth among 20 species captured (a total of seven out of 1,595 bats) in the Mogollon Mountains of eastern Arizona and western New Mexico, where they were most often captured in evergreen forest above 2,134 meters (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, they ranked twelfth of 19 species (nine captures among 1,004 individuals), but were only taken at one site, located in pine-spruce-fir forest at 2,500 meters elevation (Jones and Suttkus, 1972). Twelve spotted bats were captured over ponds, streams, and along cliff faces at four sites in the Jemez Mountains of New Mexico, ranging from 2,012 to 2,729 meters elevation and including piñon-juniper woodland, ponderosa pine, and mixed conifer forests; this was the fourth least frequently captured of 15 species and 1,532 bats netted in the region during 1995–1997 (Bogan et al., 1998). Echolocation activity of these bats was detected in riparian, conifer, piñon-juniper, and previously (20 years) intensely burned ponderosa pine habitat at the Jemez Mountains study area, but was most common in conifer and previously burned areas (Ellison et al., 2005). Also in northern New Mexico, this species ranked ninth in relative abundance among 302 bats of 10–11 species netted in mostly ponderosa pine habitat on Mount Taylor in 2006 and 2007 (Geluso, 2008). They ranked thirteenth in abundance among 16–17 species (five of 855 individuals) captured in mist nets over ponds during 1970 at Nogal Canyon in the San Mateo Mountains, Socorro County, New Mexico, in habitats described as piñon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974). They ranked seventeenth among 21 species (nine bats among 1,752 individuals) captured over water during 2006 at sites with previous records for spotted bats throughout their range in New Mexico (Geluso, 2006). Some fairly exhaustive bat faunal surveys using mist nets elsewhere in New Mexico have failed to document the presence of this species (for example, Chung-MacCoubrey, 2005; Geluso and Geluso, 2012).

Texas: At Big Bend National Park in Texas, this species ranked fourteenth in relative abundance among 18 species (54 out of 4,807 bats captured) documented in surveys conducted during 1967–1971, and were found in lowland shrub desert and river floodplain/arroyo habitats near cliff walls (Easterla, 1973). They were rarely captured (two among 1,978 captures of 17 species) in a subsequent study during 1996–1998 that emphasized surveys in lowland habitat at the park (Higginbotham and Ammerman, 2002).

Central Rocky Mountains: Spotted bats were the second to least abundant bat (10 captured) during mist netting of 1,996 bats of 15 species in piñon-juniper woodland, ponderosa pine, and mixed conifer forests at Mesa Verde National Park in southwestern Colorado (O'Shea et al., 2011a). In western Colorado, this species was the least abundant of 16 species (one among 899 bats) captured at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Spotted bats were the least frequently captured (one bat taken at 2,363 meters) among 572 bats of 15 species netted over water at multiple vegetation zones in the Henry Mountains of Utah (Mollhagen and Bogan, 1997). They ranked thirteenth in abundance (16 captures out of 1,377 bats of 15 species) in mist-netting surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016). At Arch Canyon on the Colorado Plateau in southeastern Utah, this species ranked seventh in abundance, with 11 bats captured out of 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016).

Foraging and Dietary Analysis.— Black (1974) suggested that these bats were between, within, and below-canopy foragers. Spotted bats were often heard foraging over open meadows and wetlands near coniferous forests in the Sierra Nevada of California but not within forests or over water, and were also documented foraging at a variety of lower-elevation habitats (Pierson and

Rainey 1998b). Use of open areas over fields has also been noted in central Oregon (Rodhouse et al., 2005), and spotted bats seen foraging in Utah were described as slow and maneuverable in flight (Poché, 1981).

Sizes of foraging home ranges were estimated during short-term (seven to 13 nights) radio-tracking studies in northern Arizona during 2003 and 2005 (Chambers et al., 2011). In this study region, they mainly foraged over Great Basin desert scrub habitats and piñon-juniper woodlands at distances of 11–30 kilometers from roosts. Mean home range sizes of four individuals were large, estimated to be 297 ± 25 (SE) square kilometers, with some individuals also using more than one disjunctive foraging area during the course of tracking; foraging home ranges overlapped among individuals and spotted bats did not appear to be territorial in this study (Chambers et al., 2011). Monitoring of audible calls of this species dispersing from roosts in northern Arizona revealed that the bats used side canyons as shared commuting flight paths to travel from lower elevation roosts in cliff walls, flying upwards several hundred meters in elevation. Individuals returned to day roosts directly and rapidly after foraging and possibly night roosting for several hours, with return flight speeds of three bats estimated at 30–53 kilometers per hour (Chambers et al., 2011).

Siders et al. (1999:114) reported spotted bats as "locally common" foragers over open meadows in subalpine ponderosa pine and Douglas fir forests at elevations of 2,400–2,650 meters on the Kaibab Plateau of northern Arizona. Each night for four consecutive nights a radio-tagged lactating female returned to the same area to forage, and would stop to night roost in an aspen grove, then return to the roost 38 kilometers away in lower elevation desert habitat, traveling at an estimated speed of 50 kilometers per hour (Rabe et al., 1998b; Siders et al., 1999). This and four other radio-tagged females foraged over these meadows (two also night roosted in trees bordering the meadows) for about three hours nightly from about 2300 h to 0200 h, making round-trip excursions of 77–86 kilometers from their lower elevation roosts (Rabe et al., 1998b; Siders et al., 1999). One adult female radio tracked in ponderosa pine forest habitats in northern New Mexico foraged as far as 50 kilometers round-trip from her roost (Bogan et al., 1998).

Acoustic surveys have been used to make inferences about foraging habitat use by this species. These surveys have been conducted by monitoring for distinctive audible portions of their calls, as well as recording ultrasonic components. Storz (1995) listened for audible components at 15 sites in 12 locations in a variety of lower-elevation canyon bottom habitats of the Yampa and Green rivers at Dinosaur National Monument in northwestern Colorado and adjacent Utah. Spotted bats were heard at 13 of the 15 sites. Visual observations combined with listening revealed abrupt flight maneuvers and feeding buzzes while possibly commuting through a site. Individuals seen in more extended observations at foraging places over open meadows fed throughout the night and had foraging sessions averaging 5.5 ± 2.7 (SD) minutes ($n = 187$), and 9.0 ± 8.8 minutes ($n = 30$) (Storz 1995). Foraging bats flew in large elliptical orbits from 10 to 30 meters above ground level at the open meadows but also flew within eight meters of the mid and upper canopy levels of box elder trees in riparian zones, where they did not glean insects or fly within 0.5 meters of canopy surfaces. This species at Dinosaur National Monument did not concentrate foraging above rivers in 1993 and was not observed gleaning or hovering, but it attacked insects at a rate of about once every 2.1 minutes, a much lower rate than seen in other species (Storz, 1995). Navo et al. (1992), however, noted them foraging over rivers at Dinosaur National Monument in 1990, where they foraged at heights of 10 meters or greater, used a variety of habitats, and were rare compared to other species based on acoustic recordings. Individuals observed in central Oregon foraged at heights averaging about 20 meters above ground (ranging from about three to 50 meters), and hunted over fields, low upland slopes in juniper and sagebrush, and along the rims of cliffs (Rodhouse et al., 2005). The low frequency, long inter-pulse intervals, and low intensity calls of spotted bat echolocation have been found to be nearly undetectable by many sympatric nocturnal moths (Fullard and Dawson, 1997) and are consistent with a long-range prey detection strategy and the observed habits of foraging over open places (Woodsworth et al., 1981; Storz, 1995).

Leonard and Fenton (1983) observed spotted bats foraging during 1981 in the Okanagan Valley of southern British Columbia. The bats spent most of their foraging time over old fields and hay meadows that were near ponderosa pine forests, but they only used the forest or burned forest for commuting, and seldom foraged over open river or orchards (other observations in the region suggested that open ponderosa pine woodlands were also used for foraging [Woodsworth et al., 1981; Wai-Ping and Fenton, 1989]). The bats foraged about 68% of the time in long (40 to 70 meters) elliptical orbits about 10 meters above ground, but at other times they used less predictable patterns (Leonard and Fenton, 1983). Foraging periods were variable and ranged from 11.6 ± 10.6 (presumed SD) min in May to 6.8 ± 5.3 (presumed SD) min in August; bats often dove within one meter of the ground while chasing prey but were never seen gleaning (Leonard and Fenton, 1983). Foraging activity was not strongly affected by moonlight (Leonard and Fenton, 1983; Wai-Ping and Fenton, 1989).

Spotted bats in British Columbia were calculated to attack insects every 44.5 s, with an estimated 87.5% success rate (Wai-Ping and Fenton, 1989). Three radio-tracked adult females in southern British Columbia returned to individual foraging areas via the same commuting corridors each night for four to nine nights of continuous tracking in 1986–1987, and foraging areas overlapped among individuals (Wai-Ping and Fenton, 1989). These bats flew continuously during foraging with no evidence of gleaning and only stopped during downpours. Foraging areas were elliptical in shape, 200–300 meters long, and at heights of five to 15 meters above ground; times of returning to the roost after foraging were variable, but emergence times showed little variability. Foraging areas were more predictable from night to night during early to mid-summer than during early August and later (Wai-Ping and Fenton, 1989).

Foraging spotted bats sometimes reacted seemingly aggressively to playbacks of recordings of calls of other bats but not to playbacks of other sounds (Leonard and Fenton, 1984). These and other preliminary observations of foraging bats indicated to several investigators that these bats feed solitarily and may defend boundaries of foraging areas with agonistic vocalizations if other spotted bats approach within about 50 meters (Woodsworth et al., 1981; Leonard and Fenton, 1983, 1984; Storz, 1995). Although mutual avoidance and solitary foraging is well supported by observations, there is little evidence for true foraging territoriality centered on specific locations, and some investigators have reported several individuals sometimes sharing a foraging area (Wai-Ping and Fenton, 1989; Navo et al., 1992; Pierson and Rainey, 1998b; Chambers et al., 2011; see above).

Ross (1961) examined 18 guano pellets and found no prey items other than lepidopterans, with remains of 21 moths estimated to be about eight to 12 millimeters in length. Ross (1964, 1967) further examined stomach contents of five bats from New Mexico collected by Clyde Jones and again only detected moths, at an estimated size range of five to 11 millimeters. Eighteen fecal pellets from six individuals captured in New Mexico during 2006 had 97.5% lepidopterans by proportional volume (Geluso 2006, 2017). Two stomachs of bats collected by mist net over water at 2,300 meters elevation in southern Utah contained only remains of moths about 10 millimeters in size (Easterla, 1965). Moths constituted 97% of prey volume in stomach contents of 15 bats collected at Big Bend National Park in Texas during 1971, with two bats also containing adult June beetles (Easterla and Whitaker, 1972). Lepidoptera were also predominant in stomach contents of eight bats from southern Utah (Poché, 1981). A small sample of fecal pellets of bats sampled in southern British Columbia also consisted mainly of lepidopterans, with one small beetle also noted (Wai-Ping and Fenton, 1989). A spotted bat released during daylight was observed dropping to the ground and capturing a grasshopper (Poché and Bailie, 1974).

In the most extensive analysis to date, fecal samples were examined from 33 individuals captured in northern Arizona and stable carbon and nitrogen isotopic signatures of prey were used in combination with prey identification to infer dietary habits (Painter et al., 2009). Lepidopterans were over 99% of the diet by volume in two separate summers, and isotopic composition of feces indicated that most of the insects consumed by this species were moths of the families Noctuidae, Lasiocampidae, and Geometride (Painter et al., 2009).

Roosting Habits.— Winter Roosts: Observations of winter roosts in caves or mines are limited. Four individuals were observed hibernating in a cave above a pool in Kane County, Utah during February 1930 (Hardy, 1941), one spotted bat was observed in a cave or tunnel in San Bernardino County, California in 1948 (Parker, 1952), and more recently, Geluso (2000) reported four records of solitary individuals from two caves in Nevada. Mead and Mikesic (2001) described use of a cave in northern Arizona by this species during warm months but did not verify its use as a winter roost. Sherwin and Gannon (2005) reported use of a warehouse in Albuquerque, New Mexico by a solitary spotted bat during three winters.

Given the warm season roosting habits of spotted bats (see below) it is likely that they may favor deep rock crevices for winter roosts similar to those used in summer (see below). They have been captured drinking during winter at ambient temperatures as low as -5ºC at water sources in washes in southwestern Utah near roosting places in cliffs; these pools were also used for drinking during warmer months, suggesting local hibernation (Ruffner et al., 1979; Poché, 1981).

Warm Season Roosts: Spotted bats roost primarily in crevices in cliffs and canyon walls. Easterla (1970, 1973) first noted the likelihood that these bats were cliff-crevice roost specialists based on observations of individuals in flight in Texas, and by following 13 bats by eye as they flew to cliffs and crevices after release in early morning daylight at Big Bend National Park. Roosts of three solitary individuals were located in southwestern Utah by searching for and inspecting crevices in cliff faces with mirrored sunlight, but none were found roosting during searches of local caves (Poché, 1981). Several others captured in this area and in adjacent Arizona were released and followed with binoculars as they flew towards cliff walls, with some seen alighting on vertical surfaces and entering rock crevices (Poché and Bailie, 1974; Poché and Ruffner, 1975; Poché, 1975, 1981).

Eight roosts of five spotted bats were found by radio tracking for five to 14 days each in the Jemez Mountains of New Mexico during summers 1995–1997. Roosts were located in crevices in cliffs from seven to 21 meters or more above ground (Bogan et al., 1998). Colony sizes ranged from one to 30 bats, elevations ranged from 2,005 to 2,287 meters, distances from initial capture point ranged up to 17.6 kilometers, and cliffs with roosts were southeast-facing (Bogan et al., 1998). Six of seven individuals were radio tracked to roosts at Mesa Verde National Park in southwestern Colorado in 2006–2007; they roosted exclusively in crevices in cliff faces on steep canyon walls 10–15 meters high at a distance averaging 10.8 ± 3.8 (SD) kilometers from the point of capture and an average elevation of 1,968 ± 44 (SD) meters (O'Shea et al., 2011a). Emergence counts at two widely separated roosts at Mesa Verde suggested colony sizes of 12 and 18 bats.

Five lactating females were radio tracked to five separate roosts after being captured while foraging over meadows in subalpine ponderosa pine and Douglas fir forests at elevations of 2,400–2,650 meters on the Kaibab Plateau of northern Arizona (Rabe et al., 1998b; Siders et al., 1999). Roosts were located high on cliffs 38 to 43 kilometers from the point of capture in remote areas of Grand Canyon National Park or the Kanab Wilderness Area, all in Sonoran Desert habitat at 700–1,080 meters elevation. Colony size estimates were not possible. Similarly, one female and five males radio tagged on the Arizona strip in extreme northwestern Arizona roosted in cracks, crevices, or holes in upper portions of tall cliffs where exit counts were not possible (Herder, 1998). Mead and Mikesic (2001) reported on a cave in northern Arizona used by spotted bats, noted six to nine bats roosting in a crevice in the ceiling of the cave during summer, and netted 11 bats (nine adult males, two females) at the cave entrance over the course of a night during August; they also inferred long-term use of this cave by the species based on mummified remains and a fossil. Four adult males were captured and radio tagged at this cave in summer 2003, but did not return during tracking (Chambers et al., 2011).

Chambers et al. (2011) located 14 summer roosts of 12 individuals at three study areas across northern Arizona. Roosts were in cracks or crevices in upper sections of tall vertical cliffs that were between 130 and 850 meters in height within the rugged landscapes of Grand Canyon National Park, Vermilion Cliffs National Monument, Navajo Nation property, and Canyon de Chelly National Monument. Little roost switching was apparent: over a 10-day tracking period tagged bats used an average of only 1.4 roosts (Chambers et al., 2011), similar to findings of 1.6 roosts over a nine-day period in New Mexico (Bogan et al., 1998). Spotted bat roosts in the northern Arizona study were located at distances up to 36.3 kilometers from the point of capture, and averaged 5.8 ± 1.9 (SE) kilometers (range 0.4–18) from the nearest perennial water source (Chambers et al., 2011). Seven females (six lactating or pregnant) were tracked to separate roosts, and all roosts faced in southerly directions, whereas aspects of five separate roosts of five males did not differ from random. Skin temperatures monitored for three bats tracked to roosts declined only 2.2 to 2.9ºC within the roosts, indicating little use of deeper daily torpor at this phase of the seasonal cycle (Chambers et al., 2011). Although the ability to count bats at emergence was limited, this species in the northern Arizona study did not seem to roost communally but mostly roosted as solitary adults. Two bats (one adult male, one post-lactating female) tracked to separate roosts in rock crevices in cliffs in the Okanagan Valley of southern British Columbia during August also roosted solitarily (Leonard and Fenton, 1983). Roosts in the Okanagan Valley were occupied regularly until late summer, when use became less predictable (Wai-Ping and Fenton, 1989).

Roosts in Buildings: Although colonies of spotted bats have not been reported from buildings, there are rare reports of solitary bats found on porches (Hardy, 1941; Benson, 1954; Handley, 1959), on a screen door (Rodeck, 1961), in a garage (Bleich and Pauli, 1988), under eaves of a schoolhouse (Durrant, 1935), in a warehouse (Mickey, 1961), and in 1903 and 1922 single individuals flew into research laboratories on two campuses (Hall, 1935; Vorhies, 1935). Sherwin and Gannon (2005) reported use of a warehouse in Albuquerque New Mexico by a solitary bat and reviewed other occurrences of this species in buildings. Hall (1946) reported a solitary bat in a root cellar in Esmeralda County, Nevada, and several modern records of individuals taken among tall buildings in Reno and Las Vegas in Nevada suggested these structures may have been perceived as cliff faces by the bats (Geluso, 2000).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Litter size is one, based on three observations of single births (Easterla 1971, 1976), and one embryo reported in a pregnant spotted bat in Nevada (Geluso, 2000). Two lactating females had enlarged uterine horns on just one side (Findley and Jones, 1965).

The limited available data from bats captured while foraging or drinking suggest natality may be high under typical conditions. Twenty-two among 26 (85%) adult females captured foraging in northern Arizona during summers 2003–2007 were either lactating or pregnant (Chambers et al., 2011), and 17 of 24 (71%) adult females captured over water in Big Bend National Park, Texas during summers 1967–1971 were reproductive (Easterla, 1973). In New Mexico, each of six adult females captured over water in the Sacramento Mountains were lactating (Perry et al., 1997), and five of seven (71%) adult females captured while foraging in the Jemez Mountains during summers 1995–1997 (including a drought year) were reproductive (Bogan et al., 1998). However, Geluso (2008) reported only one of four (25%) adult females captured on Mount Taylor in New Mexico as reproductive: two non-reproductive and one lactating adult taken in the drought year of 2006, and one non-reproductive female taken the subsequent summer. All of five adult females (100%) captured over water in ponderosa pine forest during June 1960 and 1963 in the Mogollon Mountains of western New Mexico and adjacent Arizona were lactating (Jones, 1961, 1964; Findley and Jones, 1965). Five of eight (63%) adult females taken at Mesa Verde National Park in Colorado during 2006 and 2007 (including a drought year) were reproductive (O'Shea et al., 2011a), four to five of six (67–83%) adult females captured over water in southwestern Nevada in 1995 and 1996 were reproductive (Geluso, 2000), and each of three adult females taken in nets over water in southern Utah during August 1964 were lactating (Easterla, 1965). The proportion reproductive for the cumulative total females taken over water at all U.S. locations and years was 77% (68 of 89 bats).

We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction in spotted bats, such as age at first reproduction and interbirth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Little is known about causes of mortality in spotted bats. Deaths due to rabies have been documented (for example, Medeiros and Heckmann, 1971; Constantine, 1979, 1988; Constantine et al., 1979; Mondul et al., 2003). Liver and lung pathology of unknown etiology were reported in a rabies-negative spotted bat (Constantine, 1961b). A live spotted bat was observed being stung by yellow jacket wasps while on the ground during the day in Yosemite National Park, California, and was later found disabled (Parker, 1952). Ectoparasites have been described but without associated mortality (for example, Whitaker and Easterla, 1975; Poché, 1981). Avian predation has been noted. Three spotted bat skulls were recovered from regurgitated spotted owl (*Strix occidentalis*) pellets at Mesa Verde National Park in Colorado (Chung-MacCoubrey and Bogan, 2003), and a spotted bat released unnaturally in daylight was taken by an American kestrel (*Falco sparverius*; Black, 1976).

Population Trend: Thirteen sites that had historical records of this species in New Mexico were revisited at the same time of year during 2006 to determine presence or absence of this species based on mist net captures or vocalizations: 11 (85%) of the sites had evidence of continued presence, with the proportion of spotted bats captured similar to earlier studies (Geluso, 2006, 2017).

Population Genetics: Preliminary analyses of 17 microsatellite loci from 31 individuals from northern Arizona do not indicate important conservation issues concerning genetic diversity of this species (Walker et al., 2014).

Management Practices and Concerns.— Earthen ponds constructed for livestock use appear to be important sources of water for spotted bats, and maintenance of water in these ponds during times of drought has been recommended (for example, Mollhagen and Bogan, 1997; Chambers et al., 2011; Bogan and Mollhagen, 2016; Geluso, 2017).

Eumops perotis californicus — Greater bonneted bat (Family Molossidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2010a, 2011b, 2017): Sensitive Species (Arizona, California, Nevada state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Species Rounded Global Status G4, Apparently Secure; Subspecies Rounded Global Status T4, Apparently Secure.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest

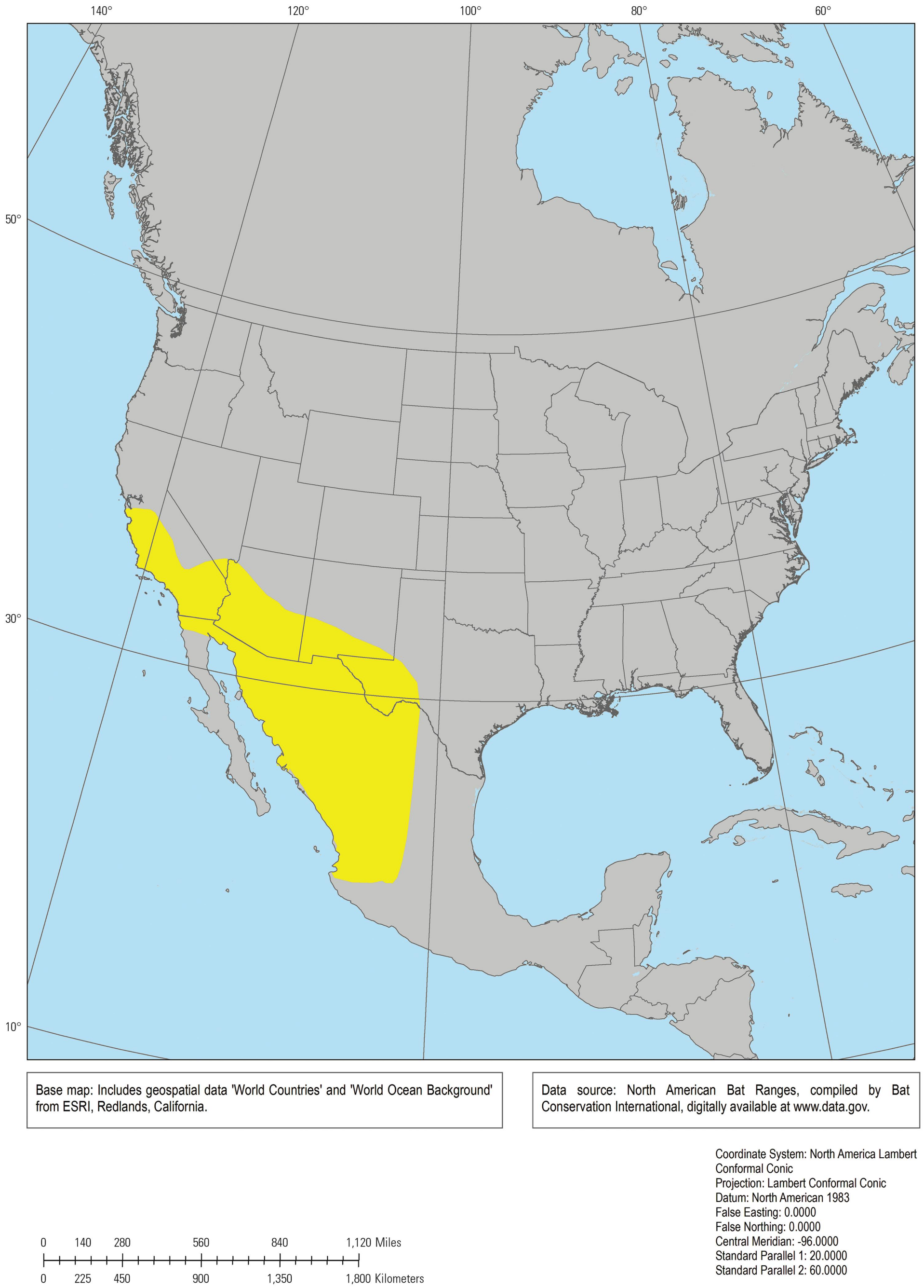
Conservation Need. California Department of Fish and Wildlife (2017): Special Animals List, Species of Special Concern. Nevada Department of Conservation and Natural Resources (2015b): Sensitive Mammal, Critically Imperiled. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need.

FIGURE 13. Greater bonneted bat, *Eumops perotis* (photo by J. Scott Altenbach).

DESCRIPTION.— The greater bonneted bat (Fig. 13) is the largest bat found in the continental United States. The forearm length ranges 73 to 83 millimeters, wingspan ranges 530 to 570 millimeters, and body masses up to 73 grams have been recorded (Barbour and Davis, 1969; Eger, 1977; Best et al., 1996). Unlike many species of U.S. bats, males are slightly larger than females (Eger, 1977). The greater bonneted bat is a typical molossid bat in morphology, with the distal half of the tail free from the interfemoral membrane, long narrow wings, and large rounded ears that are not erect. The ears are joined at the midline and extend forward beyond the nose, acting as crude airfoils 1.5 times as wide as high (Vaughan, 1959). Coloration varies from gray to brownish gray, with melanism also reported (Krutzsch, 1955). A gland is present on the throat and can be well-developed seasonally in males (Howell, 1920b; Krutzsch, 1955).

DISTRIBUTION AND SYSTEMATICS.— In the United States, the greater bonneted bat has been reported in California, Nevada, Arizona, southern New Mexico, and southern Texas (Fig. 14; Cockrum, 1960; Rowlett, 1972; Best et al., 1996). Formerly thought to be limited to the southern part of the state, acoustic surveys have confirmed their occurrence at multiple locations in northern and central California, including the Sierra Nevada and Coast Ranges, with some colonies likely resident year-long (Pierson and Rainey, 1998c). Additional records from much of California also have accumulated based on specimens submitted for rabies diagnostics (Constantine, 1998a). One subspecies is recognized in North America, *Eumops perotis californicus*, and two subspecies in South America (Best et al., 1996). Best et al. (1996) provided a complete taxonomic synonymy of past scientific names applied to the greater bonneted bat. The generic name *Eumops* comes from the Greek word meaning "good" and the Malay word meaning "bat". The specific epithet *perotis* comes from the Latin word for "through" and the Greek word for "ear". Other English common names include greater western mastiff bat, greater mastiff bat, western bonneted bat, western mastiff bat, and California mastiff bat.

HABITATS AND RELATIVE ABUNDANCE.— The greater bonneted bat has commonly been reported from desert life zones in the southwestern U.S., with elevation ranges from 60 meters below sea level in California to 1,100 meters in Texas, but it also is found in forested areas (Best et al., 1996; Pierson and Rainey, 1998c; Siders et al., 1999). Roost locations have been found in chaparral and



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 14. Approximate distribution of the greater bonneted bat, *Eumops perotis*. Species range is shown in yellow, but may extend farther south in Mexico and additional subspecies are found in South America.

live oak hillsides, xeric scrubland, and near riparian vegetation as well as in ponderosa pine habitats of the Sierra Nevada in California (for example, Vaughan, 1959; Pierson and Rainey, 1998c). Acoustic surveys in mountain ranges in California suggest that these bats shift seasonal distributions down drainages to lower elevations in winter (Pierson and Rainey, 1998c).

Despite being a fast-flying bat with relatively low maneuverability, this species is not usually captured over water during extensive mist-netting surveys of bat faunas within its known range, indicating a patchy distribution (for example, Cockrum et al., 1996; Pierson et al., 1996b). However, it was the fourth most common species (83 among 1,052 bats of 15 species) taken over water at one site in Big Bend National Park in Texas during 1967–1971, where it was captured at only three sites out of 32 netting locations; all three sites were in river floodplain and shrub desert habitats below 1,220 meters elevation (Easterla, 1973). In a subsequent study during 1996–1998, it ranked sixth in abundance at Big Bend National Park overall (88 among 1,978 bats of 17 species), where it was taken at only three sites, all in lowland habitats on the river flood plain (Higginbotham and Ammerman, 2002). The greater bonneted bat ranked sixth of 17 species (18 individuals among 390 bats) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999 (Pierson et al., 2001).

Eight lactating females were captured over water in meadows in ponderosa pine and Douglas fir forests at elevations of 2,400–2,650 meters on the Kaibab Plateau of northern Arizona in 1995; ten other individuals were also captured in the same habitat over the next two years, ranking fifth in relative abundance out of 96 captures of nine species (Siders et al., 1999; Melissa S. Siders, Bureau of Land Management, written commun., 2017). They ranked fifteenth in abundance among 17 species of bats (three captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998).

Foraging and Dietary Analysis.— This bat has a wing morphology adapted for rapid, long-distance flight, especially in open areas. The short velvet-like pelage may be an adaptation to reduce drag during flight. It is apparently the fastest flying of the U.S. molossid bats (Vaughan, 1966). Flight behavior of the greater bonneted bat was reported by Vaughan (1959). They typically emerge late into evening darkness, uttering loud, shrill calls and smacking sounds prior to and upon emergence. Bats often emerge singly at irregular intervals over periods of up to two hours. Steep dives of some 3 to 6 meters may be made before individuals pull upward and engage in level flight. Bats in flight make single-note high-pitched chirps every two to three seconds. They may fly at great heights. Vaughan (1959) observed bats flying to heights of 300 meters before being lost from view, and based on faintness of cries suggested that elevations as high as 900 meters above ground were obtained, although in other instances they were observed flying 30 to 60 meters above ground and water. They may fly great distances, and observations in southern California support the idea that weather in coastal regions may influence bats to forage in the interior over the Mojave Desert on any given night (Vaughan, 1959). Bats sometimes return to colony sites and make repeated dives at the entrance during the middle of the night. Much remains to be learned about the feeding ecology of this species, but in some areas this species appears to favor feeding over open areas, meadows, and reservoirs (Pierson and Rainey, 1998c; Siders et al., 1999).

Morphological specializations of the head and limited information on food habits suggest that this species feeds primarily on moths (Freeman, 1979). However, items reported from analysis of 43 fecal pellets and stomach contents of four bats from Arizona were primarily small (eight millimeters in length) insects, mostly hymenopterans but also including beetles, moths, and dragonflies (Ross, 1961). The large number of small-bodied insects reported from western Arizona is consistent with Vaughan's (1959) hypothesis that in southern California these bats will feed on small, light insects carried high aloft by warm updrafts. Nonetheless, further analysis of gastrointestinal tracts of nine additional individuals from Arizona showed predominantly large (60 millimeters) sphinx moths as prey (abdomens only), although ingesta also included leafhoppers, other homopterans, a cicada, and a planthopper (Fulgoridae; Ross, 1964, 1967). Easterla and Whitaker (1972) also reported large moths as predominant food items, constituting about 80% of the volume in stomachs of 18 bats collected in Big Bend National Park in Texas during 1971, but also noted the occasional presence of crickets and grasshoppers.

Roosting Habits.— Early researchers found the first known roosts of these bats in the United States in buildings in southern California (Stephens, 1906; Grinnell, 1918; Howell, 1920b). Although Howell (1920b) found colony sizes numbering 13–70 individuals roosting in buildings in this region, he suspected that their natural proclivity was to roost in rock crevices or cavities in high limbs of trees. Since then, natural roosts of *Eumops perotis* found in the U.S. primarily have been located in deep crevices in cliffs and rock outcrops, with colony sizes generally small and within the range noted by Howell (1920b). Roosts described in California in the 1930's to 1950's were in vertical crevices in granite or sandstone cliffs, with openings more than 4.5 meters above bases and varying in width from seven to 45 centimeters (Dalquest, 1946; Krutzsch, 1955). Colonies make considerable chattering and squawking sounds from within roosts during warmer parts of the day (for example, Krutzsch, 1955; Vaughan, 1959). Numbers of greater bonneted bats using any particular roost can vary from day to day and shifting of roost sites within local areas has been reported (Krutzsch, 1955; Ohlendorf, 1972), although some roosts are often occupied year after year (Krutzsch, 1955). One roost along the Kern River in central California that held an estimated 100 bats in 1948 was documented with about 75 bats in 1994, and a roost in San Diego County that was occupied in 1937 appeared to be used in 1991, indicating long-term occupancy (Pierson and Rainey, 1998c). Females with young are known to occupy roosts simultaneously with adult males (Howell, 1920b). Other species of bats often roost in the same or nearby crevices. Solitary individuals, presumed wanderers or stragglers, have been observed on trees, sides of buildings, under awnings and in other atypical, temporary situations (von Bloeker, 1932; Krutzsch, 1955).

Little is known about seasonal differences in roost utilization, but these bats are not known to undergo deep winter hibernation (Leitner, 1966). Greater bonneted bats are very active and alert within roosts during warmer months in California, where during December through February they are known to enter daily torpor and arouse in the evenings to emerge and feed nightly, except on cool nights when air temperature was below 5ºC (Leitner, 1966). Howell (1920b) observed shallow torpor in this species and reported that the bats could remain torpid in their roosts for several days during extended periods of cool winter weather in southern California. Although some roosts may be used year-round, there is also evidence for some switching from summer roosts to other locations during winter (Krutzsch, 1955).

Openings to rock crevices used as roosts can be horizontal or vertical (Krutzsch, 1955). Because of their low maneuverability and fast flying speed, they occupy crevices with unobstructed approaches and openings high above ground (Howell, 1920b; Krutzsch, 1955; Vaughan, 1959). Well-used colony sites are marked by urine stains on cliff faces and accumulations of guano below. In an extensive study in California, Vaughan (1959) found these bats in 22 such crevices, all of which were vertical, nearly vertical, or situated on steep slopes. Crevices used as roosts were more than 0.3 meters deep and usually more than three meters deep, with entrances at least five centimeters wide and 15 centimeters long at the bottoms or sides of the crevices. Most of these were in large, exfoliating slabs of rock in granite or consolidated sandstones. Similarly, in southwestern Texas a colony of 71 greater bonneted bats roosted in a high crevice formed by exfoliating rimrock (Ohlendorf, 1972).

The only two roosts known in Arizona in the early 1960's were maternity colonies in widely separated parts of the state. One housed 15–20 bats in an up to 12–centimeter-wide crevice in the roof of a shallow, 14– to 15–meter high grotto in a 100 meters high cliff in southeastern Arizona; a group of 90–100 occupied a roost in a crevice opening 20 meters high in the roof of a second shallow grotto in a 100 meters high cliff in northwestern Arizona (Cockrum, 1960; Cox, 1965; Cockrum et al., 1996). From two to four individuals also were seen emerging from a crevice in the roof of a cave that housed cliff dwellings at Tonto National Monument in Gila County in south-central Arizona during 1962 (Johnson and Johnson, 1964). General daytime locations of roosts of three adult females radio tagged on the Kaibab National Forest in northern Arizona were in Sonoran Desert habitat (about 600–880 meters elevation), within inaccessible high cliffs along the rim of the Grand Canyon, 28–29 kilometers from the points where the bats were captured over ponds in subalpine forest at 1,900–2,400 meters elevation (Siders et al., 1999). One of the radio-tagged individuals was tracked to a tall ponderosa pine tree for a single night before moving to a roost at an unknown location within the Grand Canyon (Siders et al., 1999).

Greater bonneted bats are also known to roost in attics and buildings, particularly in crevice-like spaces, and historically were reported from such places near Los Angeles, California (Howell, 1920b, von Bloeker, 1932; Krutzch, 1955; Leitner, 1966; Couffer, 1992). Reproduction occurred in these buildings, including a maternity colony with 25 young described inhabiting the attic of a three story building in Covina, Los Angeles County, California (Howell and Little, 1924). They also have been observed in or near other cities, including Tucson, Arizona, Las Vegas, Nevada, and Mexico City, Mexico (Cockrum, 1960; Bradley and O'Farrell, 1967; Avila-Flores and Fenton, 2005). Night roosting of solitary individuals has been observed (Krutzsch, 1955).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Hilda Grinnell (1918) recorded single embryos in each of three adult females examined in southern California. Howell (1920b) reported single embryos in each of 13 females taken in southern California, as did Krutzsch (1955) based on notes of others on an unspecified number of females. However, Krutzsch (1955) also directly observed one female with two embryos and four with one embryo each. One female from southern Arizona was observed giving birth to a single young in the field (Cockrum, 1955, 1960). Two females with single embryos were collected in Capote Canyon in southwestern Texas (Ohlendorf, 1972), and single embryos were found in each of 6 pregnant females examined at Big Bend National Park in Texas, where natality was 56% (20 of 36 adult females captured over water were reproductive; Easterla, 1973). Six of eight females captured over water near the Grand Canyon in northern Arizona were lactating (Siders et al., 1999). In northwestern Arizona, each of four adult females taken at a maternity roost was lactating (Cockrum, 1960). Birth occurs once annually during warm months but timing is otherwise asynchronous within a colony (Krutzsch, 1955). We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as age at first reproduction and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Little is known about causes of mortality in greater bonneted bats. Deaths due to rabies have been documented (for example, Constantine et al., 1979; Constantine, 1979, 1988; Caire and Loucks, 2013). A peregrine falcon was observed preying on a greater bonneted bat released during daylight (Easterla, 1973). Ectoparasites are known (for example, Krutzch, 1955) but no associated mortality has been reported.

Population Trend: Howell (1920b:111) stated: "I have no hesitancy in pronouncing it a common species in the orange section or thermal belt of Los Angeles County. However, to be successful in finding it, one must employ no little energy and perseverance." Other than the work of Dalquest (1946), Krutzsch (1955), and Vaughan (1959), few such efforts were employed in California until the early 1990s, when previously known roosting areas and likely sites throughout California were visited by Pierson and Rainey (1998c) to search for this species and to monitor for their distinctive echolocation calls. They confirmed the continued occurrence of greater bonneted bats in many regions and added additional distribution records. However, few colonies were observed directly, and all colonies were small (less than 100 individuals). Possible switching among alternate roosts and the capability of individuals to forage over great distances may possibly inflate their seeming abundance.

Greater bonneted bats were confirmed in flight during the 1990s at a site in the Coast Range in San Benito County, California where a roost was known to exist in 1940 (Dalquest, 1946), but the crevice utilized at that time had since eroded away (Pierson and Rainey, 1998c). In the Sierra Nevada, a roost on the Kern River which was occupied by about 100 bats in August 1948 was occupied by up to 75 bats in 1992. About seven new roost sites with colony maxima of about 60 bats were also located near Fresno and Jamestown, California. They were commonly detected in the central Sierra Nevada during the 1990s, where two roosts with evidence of breeding colonies were found (Pierson and Rainey, 1998c). In southern California, however, findings suggested serious reductions in populations in some areas, particularly the northern Los Angeles basin. In the latter area, places where these bats were common up through the 1960s lacked evidence for their occurrence in the 1990s. Only one roost previously known to have bats was found occupied. Numbers at this roost had dropped from 40–50 adults in 1969 to three bats in 1992.

Based primarily on acoustic surveys, Pierson and Rainey (1998c) reported that greater bonneted bats still occur in western Riverside and San Diego Counties, California. Locations where three small (10–12 bats) colonies occurred in this region were determined in the early 1990s. One of these had been occupied in the 1940s. A fourth site where Vaughan (1959) had described an active colony no longer had evidence of bats, and was occupied by a housing subdivision.

MANAGEMENT PRACTICES AND CONCERNS.— As with other bats not commonly represented in museum collections, requests for permits for scientific collecting should be reviewed carefully to insure that the activities do not pose a direct threat to colonies, as occurred with this species in the past. Cox (1965) for example, reported acquiring specimens from one of the only two known maternity colonies in Arizona by shooting into the roost crevice opening, as did Cockrum et al. (1996) at one of these sites during the 1960s, and Ohlendorf (1972) at a Texas colony.

Many of the old buildings that provided suitable roosts for the greater bonneted bat in southern California have been razed (Pierson and Rainey, 1998c). These large bats can be noisy and obvious when roosting in buildings, stimulating attempts to exterminate them. The only two colonies known to exist in public buildings in southern California were partially exterminated by public health personnel as recently as 1991 (Pierson and Rainey, 1998c), and homeowners in California were reported to have killed 20–30 individuals during an exclusion attempt because they roosted in an attic and were considered nuisances (Howell, 1920b).

Impoundments that submerge cliff faces can eliminate roosting habitat. Mining and quarrying at cliffs and the construction of roads and bridges through cliff-walled canyons can impact colonies of these and other cliff-dwelling bats through blasting; in some areas recreational climbing can also increase disturbance (Pierson and Rainey, 1998c). An analysis of likely acceptance of gates by bat species based on wing and echolocation characteristics suggested greater bonneted bats might abandon roosts fitted with bat gates (Tobin and Chambers, 2017).

NOTES AND COMMENTS.— During World War II, a secret U.S. government program was aimed at using bats to carry small incendiary weapons; the principal investigator kept a pet greater bonneted bat nicknamed “Flamethrower” that accompanied him during outings in the field, sometimes resting on his shoulder (Couffer, 1992).

Eumops underwoodi — Underwood's bonneted bat (Family Molossidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G4, Apparently Secure.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need.

Description.— Underwood's bonneted bat (Fig. 15) is the second largest bat in the United States, being only slightly smaller than the greater bonneted bat (see account above). Underwood's bonneted bat is distinguishable from the greater bonneted bat externally based on the presence of stiff bristles (guard hairs) on the rump in *E. underwoodi*. Ears are set close together but are not joined on the forehead. Upper lips are smooth. As in other molossids, the tail is free from the interfemoral membrane, the ears are large, rounded and extended forward, and the wings are long and narrow. The dorsal pelage can be various shades of brown, whereas the ventral pelage tends to be gray. Body mass of Arizona specimens range from 53.0 to 65.3 grams (Cockrum and Gardner, 1960), and forearm lengths 66.9–73.7 millimeters (Hoffmeister, 1986). Unlike many species of U.S. bats, males are slightly larger than females (Eger, 1977).

Figure 15. Underwood's bonneted bat, *Eumops underwoodi* (photo by J. Scott Altenbach).

Distribution and Systematics.— Underwood's bonneted bat is found primarily in the Neotropics, from Nicaragua north to Sonora and Baja California in Mexico and extreme southern Arizona. The latter is the only area of occurrence in the United States (Fig. 16; Kiser, 1995; Cortés-Calva et al., 2012). The first U.S. record was a specimen shot over a pond near Sasabe in Pima County, Arizona in 1954 (Baker, 1956b). The second and third U.S. specimens were taken in 1957 over water in the same region of Arizona but at the southwestern flank of the nearby (less than approximately 40 kilometers) Baboquivari Mountains (Hoffmeister, 1959), and 16 more specimens were taken by mist net in 1958 near the same location as the first record, which was a few hundred meters north of the border with Sonora, Mexico (Cockrum and Gardner, 1960). Underwood's bonneted bat has been captured in the region more frequently since the 1950s, particularly by mist net at the large, permanent Quitobaquito Spring along the Sonoran border in Organ Pipe Cactus National Monument (for example, Petryszyn and Cockrum, 1990). Quitobaquito Spring is about 130–155 kilometers west of the original capture locations near Sasabe and the Baboquivari Mountains. Hoffmeister (1970) reported that the presence of this species in southern Arizona was sea-

Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 16. Approximate distribution of Underwood's bonneted bat, *Eumops underwoodi*. Species range is shown in yellow, but may extend farther south in Central America.

sonal, from April to October. However, subsequent research found these bats present in the region during mid-winter (Petryszyn and Cockrum, 1990).

Two subspecies of Underwood's bonneted bat are recognized. *Eumops underwoodi sonoriensis* (first named as *Eumops sonoriensis* by Benson [1947] based on specimens from Sonora) is found in southern Arizona and Sonora, Mexico. *Eumops underwoodi underwoodi* occurs from Chihuahua, Mexico south to Nicaragua. Distribution and systematics are reviewed in greater detail by Kiser (1995) and Eger (1977), with a complete taxonomic synonymy of past scientific names applied to Underwood's bonneted bat appearing in Kiser (1995). The generic name *Eumops* comes from the Greek word meaning "good" and the Malay word meaning "bat". The specific epithet is a patronym in honor of Cecil F. Underwood, collector of the type specimen taken in Honduras in 1937 (Goodwin, 1940). Other English common names include Underwood's mastiff bat.

HABITATS.— In the United States, this bat is known only from near the boundary with Mexico in Pima County, Arizona (Hoffmeister, 1986). They have been taken in mist nets while drinking at a number of watering sites, catchment basins, and reservoirs in Sonoran Desert and mesquite-grassland habitats. Like other molossid bats, this species is probably capable of traveling long distances to forage, and they may migrate. In Arizona, specimens have been taken in mesquite bosque habitat (Cockrum and Gardner, 1960) near Sasabe and over Quitobaquito Pond in Sonoran desert scrub at Organ Pipe Cactus National Monument in all seasons (Petryszyn and Cockrum, 1990). Foraging habitats are noted below. In Jalisco, Mexico, they have been reported from pine-oak forests (Watkins et al., 1972), and they are also found in a variety of other habitats in the Neotropics, including tropical forest (Carter et al., 1966; Hellebuyck et al., 1985).

FORAGING AND DIETARY ANALYSIS.— Underwood's bonneted bats make loud, piercing, high-pitched audible calls while in flight. Three radio-tagged individuals captured at Quitobaquito Pond in Organ Pipe Cactus National Monument in Arizona foraged nightly over relatively flat areas of the Rio Sonoyta Valley and adjacent bajadas and slopes, and into the city of Sonoyta, Mexico, a maximum of 24 kilometers from day roosts; general observations suggested flight paths covered hundreds of kilometers per night while foraging (Tibbitts et al., 2002). Foraging habitats included Sonoran desertscrub, mesquite-tamarisk riparian areas, agricultural fields, wilderness, and residential areas; bats also foraged over steep terrain along ridgelines and hilltops (Tibbitts et al., 2002). The bats did not return to Quitobaquito Pond for water each night, presumably drinking at other sources around Sonoyta such as the large sewage treatment plant. Over the approximately five- to 13–night tracking periods of the three bats, nightly home range estimates varied from 1.0 to 284.6 square kilometers and estimated foraging areas were 100, 160, and 474 square kilometers (Tibbitts et al., 2002).

Morphological specializations of the head and limited information on food habits suggest that this species feeds primarily on beetles (Freeman, 1979). Ross (1964) reported six- to 10–millimeter beetles as the predominant food item (47%) in digestive tracts of 6 bats collected at one location on the same night in Arizona, but also noted the presence of large orthopterans (40–60 mm) at 31%, homopterans (cicadellids), and lepidopterans. One specimen from Michoacán, Mexico had fed on large (*ca.* 40–60 millimeters) June beetles and long-horned beetles, suggesting that the diet of Underwood's bonneted bat can include a diversity of types and sizes of insects (Ross, 1967).

ROOSTING HABITS.— Roosting sites in the U.S. remained undescribed for nearly 50 years after these bats were first discovered in Arizona. It had previously been speculated that they may roost in crevices in high steep cliffs (for example, Hoffmeister, 1986), similar to other molossid bats. However, in Jalisco, Mexico, a group of 13 was reported roosting in a large hollow tree (Watkins et al., 1972) and an individual was reported roosting under palm leaves in El Salvador (Hellebuyck et al., 1985). In 2001, preliminary radio-tracking studies of three individuals confirmed that bats captured drinking at the Quitobaquito Pond at Organ Pipe Cactus National Monument in Arizona roosted in secondary cavities (previously formed by an excavating animal like a woodpecker) in large saguaro cacti (Tibbitts et al., 2002; Tibbitts and Pate, 2009). The first roost found in 2001 was in a woodpecker-excavated cavity near the top of a nine-meter tall saguaro where one radio-tagged bat and two untagged bats emerged at dark. Subsequently the three tagged bats were observed resting during the day in separate cavities, often switching cavities from day to day; cavities used by any one individual were all generally within one kilometer of each other. Numbers of bats using any particular cavity varied from one to five. Underwood's bonneted bats also used woodpecker cavities in saguaros for night roosting (Tibbitts et al., 2002).

Population Ecology.— Litter Size, Natality, and Female Reproduction: One Underwood's bonneted bat taken in extreme southern Arizona had a single embryo, and all of eight adult females taken over water in July 1958 were reproductive (Cockrum and Gardner, 1960). Another female was also reported with a single embryo (Hoffmeister, 1986). One of two (50%) adult females taken in southern Arizona during May 1959 was reproductive and gave birth to a single young in captivity (Constantine, 1961a). Nine female *E. underwoodi underwoodi* captured over water in Nicaragua were all reproductive (Dolan and Carter, 1979).

We are unaware of any other detailed published information on additional aspects of the population ecology of Underwood's bonneted bat.

Management Practices and Concerns.— The maintenance of water sources known to be relied on for drinking within the limited range in the U.S. appears to be critical. These bats are believed to need large surface areas for access to drinking water due to lack of maneuverability, so that loss of water at Quitobaquito Pond and other sources of drinking water with large surfaces within their limited U.S. distribution (for example, around the Baboquivari Mountains) could be very detrimental. Over-collecting at these sites by biologists should be guarded against. Increasing human encroachment and expanded vehicular traffic near Quitobaquito Pond on Organ Pipe Cactus National Monument also is a major concern. They have been observed feeding low over the expanding nearby highway (Tibbitts et al., 2002). Deaths due to collisions with motor vehicles are gaining increasing attention as a source of mortality in bats (for example, O'Shea et al., 2016a).

Idionycteris phyllotis — Allen's big-eared bat (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2009a, 2010c, 2011a,b, 2017): Sensitive Species (Arizona, Colorado, Nevada, New Mexico, Utah state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G4, Apparently Secure.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need. Colorado Parks and Wildlife (2015b): Species of Greatest Conservation Need, Tier 2. Nevada Department of Wildlife (2013): Protected Mammal, Species of Conservation Priority. Nevada Department of Conservation and Natural Resources (2015a): Critically Imperiled. New Mexico Department of Game and Fish (2006, 2015): Imperiled, Species of Greatest Conservation Need, Sensitive. Utah Division of Wildlife Resources (2015; Sutter et al., 2005): Species of Greatest Conservation Need.

Description.— Allen's big-eared bat (Fig. 17) is distinctive among U.S. bats with long ears: it has a pair of lappets, or fleshy lobes, extending from the base of the ears to over the forehead, and lacks conspicuous glands on the muzzle. The calcar is keeled. Forearm lengths range from 42 to 49 mm and body masses 8 to 16 g (Czaplewski, 1983; Hoffmeister, 1986). Pelage coloration is

FIGURE 17. Allen's big-eared bat, *Idionycteris phyllotis* (photo by J. Scott Altenbach).

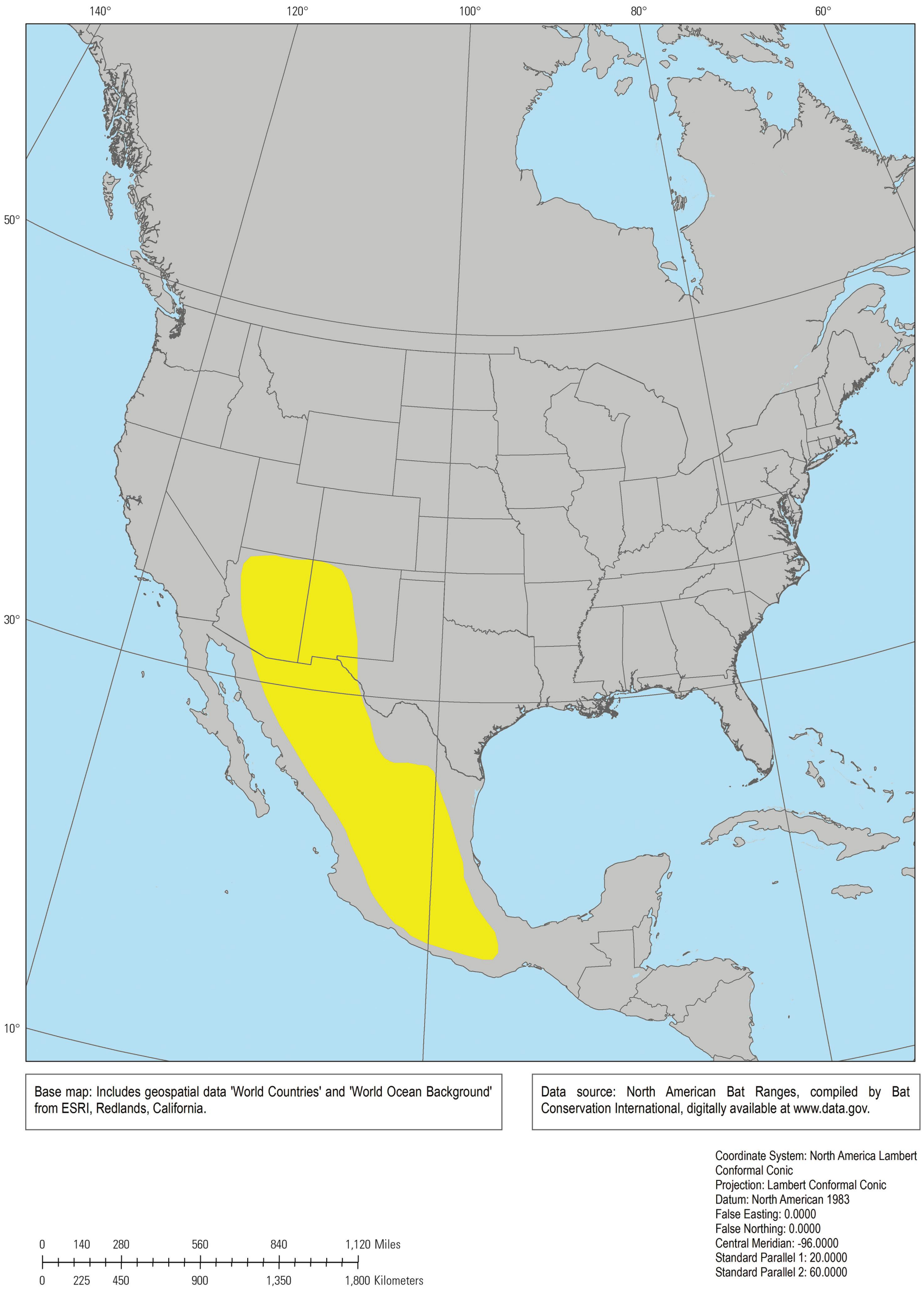
variable from light brown to almost blackish, and lighter ventrally. The bases of the hairs are black, with tips various degrees lighter, often yellowish gray; a tuft of white hair is visible near the posterior base of each ear (Barbour and Davis, 1969; Czaplewski, 1983).

DISTRIBUTION AND SYSTEMATICS.— Allen's big-eared bat occurs in the southwestern United States and Mexico south to Oaxaca (Fig. 18; Czaplewski, 1983; Bonilla et al., 1992). In the United States, it is mostly reported from middle-elevation forested habitats in southern Utah and Nevada, Arizona, western New Mexico, southwestern California (Czaplewski, 1983), and western Colorado (Hayes et al., 2009; Adams and Lambeth, 2015), although it also has been taken somewhat less frequently at both higher and lower elevations in some of these states (Hoffmeister, 1986). They are probably quite localized in distribution. The first U.S. specimen was taken in 1955 in the Chiricahua Mountains of southeastern Arizona at an elevation of 1,646 m, and prior to the Arizona record the species was only known based on two specimens taken in Mexico in 1878 and 1922 (Cockrum, 1956).

The placement of Allen's big-eared bat within the genus *Idionycteris* is a result of reliable taxonomic research during the past 25 years. Handley (1959) considered *Idionycteris* to be a subgenus of *Plecotus*. Tumlinson and Douglas (1992) and Bogdanowicz et al. (1998) subsequently provided strong evidence that the generic name *Plecotus* was valid only for certain species of Old World bats. Based on their work and suggestions of previous authors (for example, Williams et al., 1970, based on karyotypes), *Idionycteris* was elevated as the generic name for these bats, formerly known as *Plecotus phyllotis* based on Handley's (1959) analysis and originally named *Corynorhinus phyllotis* by Allen (1916). Czaplewski (1983) provided a complete taxonomic synonymy of past scientific names applied to this species. Two subspecies have been described based on morphology, size, and distribution. *Idionycteris phyllotis hualapaiensis* is smaller in size and found in the northern part of the species range in Nevada, Utah, and northern Arizona, and *Idionycteris phyllotis phyllotis* is larger in size and found in the central part of the species range, which includes the remainder of Arizona and New Mexico (Tumlinson, 1993).

The generic name *Idionycteris* is based on the Greek for "distinct" and "bat". The specific epithet originates from Greek words meaning "long" and "ear". The common name acknowledges Glover Morrill Allen, the early 20th century mammalogist and bat specialist who first described the species. Other English common names include Mexican big-eared bat, lappet-browed bat, Allen's lappet-eared bat, and Allen's lappet-browed bat.

HABITATS AND RELATIVE ABUNDANCE.— Allen's big-eared bat was discovered in the United



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 18. Approximate distribution of Allen's big-eared bat, *Idionycteris phyllotis*. Species range is shown in yellow, but extends farther north in western Colorado, southern Utah, and southern Nevada (see text).

States based on a single specimen netted over water in an oak-juniper vegetation community in the Chiricahua Mountains of southeastern Arizona in 1955 (Cockrum, 1956). During 1958 an additional 22 specimens were taken at elevations ranging from 1,082 to 1,646 meters in the Chiricahua Mountains, and another 10 specimens were collected in the nearby Galiuro Mountains (Commissaris, 1961). Habitats at these first collecting sites were described as predominantly Mexican pine-oak woodland with nearby riparian hardwoods including Arizona sycamore (*Platanus wrightii*), cottonwood (*Populus fremontii*), chokecherry (*Prunus serotina*), Arizona walnut (*Juglans major*), and willows (*Salix* sp.; Commissaris, 1961).

They also are known from piñon-juniper woodland at 1,768 to 2,134 meters in western New Mexico (Jones, 1961), varied habitats at 1,439 to 2,396 meters elevation in the Henry Mountains of southeastern Utah (Mollhagen and Bogan, 1997), and tropical deciduous forest in Oaxaca, Mexico (Bonilla et al., 1992). This species is not difficult to capture in mist nets, yet where they are captured they are usually low in abundance compared to other species (Hoffmeister, 1986), and their occurrence can be much localized. Some extensive mist-net surveys over water within the general distribution of Allen's big-eared bats in the U.S. have failed to capture this species (for example, Bogan et al., 1998; Hall, 2000; Chung-MacCoubrey, 2005; O'Shea et al., 2011a; Geluso and Geluso, 2012).

Southwestern U.S.: ***Arizona*****:** Surveys after the 1950's found Allen's big-eared bats in a wider variety of habitats than initially discovered, including: ponderosa pine forest in northern Arizona (Findley and Jones, 1961); mixed ponderosa pine, spruce, fir, and aspen forest at 2,195 to 2,377 meters in central Arizona (Hayward and Johnson 1961; Jones, 1961; Johnson and Johnson, 1964); Mojave and lower Sonoran deserts in northwestern Arizona at 792 to 1,067 meters elevation (Cockrum and Musgrove, 1964a); and riparian habitats in Arizona characterized by cottonwoods, willows and arrowweed (Hoffmeister, 1986). Allen's big-eared bats ranked tenth in abundance among 15 species (26 bats captured out of 1,673 individuals) netted over water in ponderosa pine and ponderosa pine-Gambel oak woodlands at about 2,200 to 2,600 meters elevation on the Coconino Plateau of northern Arizona during 1993–1995 (Morrell et al., 1999). They ranked eleventh in relative abundance (14 taken among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). They also were low in abundance in 2006 and 2007 at four study areas in northern Arizona ponderosa pine forests and piñon-juniper woodlands at 1,200–2,500 meters elevation, with just 32 taken among 2,090 bats of multiple species captured (Solvesky and Chambers, 2009). They ranked ninth in relative abundance (70 captures out of 3,458 individuals of 17 species) among bats captured in mist-nets set over water in Mohave County in western Arizona (Cockrum et al., 1996). They ranked tenth in abundance among 17 species of bats (12 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). Information from Arizona has suggested that reproductive females utilize habitats at higher elevations than males during summer (Solvesky and Chambers, 2009), a reversal of patterns seen in some other species of vespertilionid bats (Weller et al., 2009).

New Mexico**:** In the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were most often captured in evergreen forest above 2,134 meters, Allen's big-eared bats were low in abundance (a total of 31 among 1,595 bats of 20 species, ranking fifteenth) during 1958–1963 (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, these bats ranked eighth of 19 species (33 captures among 1,004 individuals) and were taken at two sites, one located in pine-spruce-fir forest at 2,500 meters elevation and the other in riparian hardwoods at 1,465 meters (Jones and Suttkus, 1972). They ranked thirteenth in abundance out of 16–17 species (five bats among 855 individuals) captured in mist nets over ponds during 1970 at Nogal Canyon in the San Mateo Mountains, Socorro County, New Mexico, in habitats described as piñon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974). Somewhat farther south, Jones (2016) documented bats captured during surveys of the Greater Gila region of Catron, Grant, and Sierra counties of New Mexico; they ranked second-to-least abundant, with two captures among 282 individuals of 16–17 species (Jones, 2016). This species ranked fourteenth among 21 species (15 bats among 1,752 individuals) captured over water during 2006 at sites with previous records throughout their range in New Mexico (Geluso, 2006, 2017).

Central Rocky Mountains: *Utah*: Allen's big-eared bat ranked twelfth in relative abundance of 15 species (nine individuals out of 572 bats) in the Henry Mountains of southeastern Utah, where they were netted over water at 1,439 to 2,396 meters elevation (Mollhagen and Bogan, 1997). At Arch Canyon on the Colorado Plateau, also in southeastern Utah, these bats were among the least abundant species, with one bat captured out of 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016).

FORAGING AND DIETARY ANALYSIS.— The flight of Allen's big-eared bat was described as slow and direct (Jones, 1961), although they can show agile flight in confined spaces (Commissaris, 1961). They were observed foraging around piñon pine trees at White Rock Spring, Red Rock Canyon in the Spring Mountains, Clark County, Nevada. At this location they also were seen to forage slowly, hover near vegetation, and occasionally attack small insects in or on the vegetation (Simmons and O'Farrell, 1977). They produce distinctive, loud audible calls in flight (Jones, 1961; Barbour and Davis, 1969; Simmons and O'Farrell, 1977) and were reported to fly at heights of about 10 meters above ground during general observations in New Mexico (Barbour and Davis, 1969). These bats were categorized as moth strategists and between-, within-, and below-canopy foragers in dietary analysis of bats sampled in the San Mateo Mountains of New Mexico (Black, 1974). Moths were the only dietary component noted in fecal analysis of a small sample of individuals from ponderosa pine forests of northern Arizona (Warner, 1985). Ross (1964, 1967) examined digestive-tract contents from 25 bats taken in New Mexico and Arizona. Microlepidopterans six to 12 millimeters in length were the predominant food group, but other groups also identified included beetles and flying ants, the latter suggesting opportunistic foraging on swarms (Ross, 1964, 1967). Lepidopterans constituted 98% by volume and 100% in frequency of fecal pellets sampled from 13 individuals in southwestern New Mexico, with coleopterans only a very minor component (Geluso, 2006).

ROOSTING HABITS.— Winter Roosts: Little is published about the winter roosts of Allen's big-eared bat. Three specimens were obtained from a mine in southwestern New Mexico during December (Jones, 2016). Mist netting of bats over water during winter months in central and southern New Mexico yielded only one (during March), although intermittent activity of 11 other species was detected from November to March including captures of 401 individuals (Geluso, 2007). Individuals roosting in a northwestern Arizona mine tunnel during mid- to late September were described as "sluggish" and "extremely fat" but did not use this roost during winter (Cockrum and Musgrove, 1964a:473).

Warm Season Roosts: The first roost of Allen's big-eared bats found in the U.S. was located among boulder and rubble piles within a cave in the Chiricahua Mountains of southeastern Arizona (Commissaris, 1961). About 30 individuals were observed in this situation during August 1958, along with fringed myotis and Townsend's big-eared bats; 14 Allen's big-eared bats were captured, all females and volant juveniles, indicating that the roost housed a small maternity colony. Visits to the site the subsequent year during February, May, and late August failed to find this species

(Commissaris, 1961). This species will also roost in abandoned mine tunnels. A maternity colony of about 100 adult females and juveniles occupied two nearby mine tunnels, and about 25 used a third tunnel, all in lower Sonoran desert at about 800 meters elevation and 50 kilometers from forested habitat in Mohave County, Arizona during 1960–1962 (Cockrum and Musgrove, 1964a). The main roost was subsequently destroyed due to road construction (Cockrum et al., 1996). Three adult females were radio tracked to roosts at Grand Staircase-Escalante National Monuments in southern Utah during 2004; all were found using rock crevices in the top of a high sandstone cliff in a small box canyon in piñon-juniper woodland, where estimated colony size was at least 15 bats (Siders and Jolley, 2009).

Allen's big-eared bats will form maternity colonies in tree snags. Rabe et al. (1998a) used radio telemetry to determine roosting habits of 16 adult females during the maternity season in ponderosa pine forests of the Coconino National Forest in northern Arizona. All roosted in colonies under exfoliating bark in ponderosa pine snags. Eleven of these roosts that housed maternity colonies were found 11–14 years later by Solvesky and Chambers (2009): only one held a colony (eight bats), five snags were standing but had no exfoliating bark and thus seemed unsuitable as roosts, and the remainder had fallen or were presumed cut for firewood. The total number of roosts located by both Solvesky and Chambers (2009) and Rabe et al. (1998a) was 27. All but one were under exfoliating bark of ponderosa pine snags attached at the upper horizontal ends; one roost was in a vertical crevice in a building (Solvesky and Chambers, 2009). Maternity colony sizes based on emergence counts averaged 11 individuals (range two to 21), with each of 14 radio-tagged pregnant or lactating females using one to three different roosts in a 10-day tracking period; two roosts of tagged males were in vertical sandstone cliffs at lower elevations than maternity roosts (Solvesky and Chambers, 2009). Maternity roost trees were closer to roads, taller, and in forest stands with more downed debris and greater canopy closure than comparison snags chosen at random bearings and distances from capture sites. Solvesky and Chambers (2009) speculated that forest roads might be used as flight corridors, that taller snags provide more exfoliating bark, that canopy closure may decrease cooling and winds (which could increase chances of bark sloughing), and that greater debris on the ground may be residual in areas where the bats might show higher fidelity because of formerly high snag densities. Six female Allen's big-eared bats radio tracked in east-central Arizona ponderosa pine forest roosted in three ponderosa pine snags, one Douglas fir snag, and one rock crevice, with mean colony sizes of 7 bats observed in exit counts (range up to 15; Saunders, 2015).

Allen's big-eared bats have rarely been reported roosting in buildings. A maternity roost with an unspecified number of bats was located in a vertical crevice in a residential building in northern Arizona (Solvesky and Chambers, 2009). A single male was reported roosting in the eaves of a house in Arizona (Cockrum and Musgrove, 1964a), and a single adult female was observed hanging from a rafter of a picnic shelter in western Colorado (Adams and Lambeth, 2015).

Roosting habits of male Allen's big-eared bats are poorly known. Two males in northern Arizona were radio tracked to two roosts in vertical sandstone cliff faces, but numbers of roost mates were not known (Solvesky and Chambers, 2009). Curiously, 16 were netted over a small pond in Gila County, Arizona, on three summer nights and all were males (Hayward and Johnson, 1961), perhaps suggesting the existence of nearby bachelor roosts or colonies.

POPULATION ECOLOGY.— Litter Size, Natality, and Female Reproduction: One adult female sampled in Utah contained a single fetus (Black, 1970), as did three females sampled in New Mexico (Jones, 1961; Findley et al., 1975). Each of 11 adult females captured at a maternity colony in Mohave County, Arizona during summer 1961 were lactating (Cockrum and Musgrove, 1964a). Natality rates of bats captured over water also are high based on the limited data available.

Each of two adult females captured over water near Flagstaff, Arizona in summer 1959 were lactating (Findley and Jones, 1961), all of 27 adult females captured over water in northern Arizona ponderosa pine forests in 2006 and 2007 were reproductive (including two that were post-lactating; Solvesky and Chambers, 2009), and 22 of 25 (88%) captured over water in similar habitat in the same region were reproductive in 1993–1995 (Morrell et al., 1999). All of 13 females captured over water at three locations in New Mexico during summer 1960 were reproductive (Jones, 1961), as were 24 of 25 females (96%) taken over water in the Mogollon Mountains of southwestern New Mexico and adjacent Arizona during June and July 1960 to 1963 (C. Jones, 1964). Six of 6 females (100%) captured over water in Catron County, New Mexico during 1966 were reproductive (Barbour and Davis, 1969). Two of three adult females (67%) captured over water in southern Utah were reproductive (Siders and Jolly, 2009). The proportion reproductive for the cumulative total females taken over water over all U.S. locations and years was 95% (96 of 101 bats).

We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as age at first reproduction and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Little is known about mortality factors affecting this species. A maternity colony of about 25 Allen's big-eared bats was apparently killed when vandals set fires within the mine tunnel they occupied in northwestern Arizona (Cockrum and Musgrove, 1964a). Very few have been tested for rabies infection, with none reported positive in the literature thus far (Constantine, 1979, 1988; Mondul et al., 2003; Blanton et al., 2007).

Population Trend: Seven sites that had historical records of Allen's big-eared bats in southwestern New Mexico were revisited during 2006, and all had evidence of continued presence of this species based on mist net captures or vocalizations (Geluso, 2006).

Management Practices and Concerns.— In studies of several species of bats (including Allen's big-eared bat) roosting under loose bark or in lightning-caused cracks in ponderosa pine snags in northern Arizona, Rabe et al. (1998a) recommended measures to help recruit snags with loose bark as bat roosts. They suggested that forest management should retain large trees that die in place, thin stands of small trees to allow faster development of larger trees, and kill live large trees in areas of low snag density to hasten roost development. Prescribed fire but with protection of existing snags also may help promote development of future snags (Rabe et al., 1998a). Solvesky and Chambers (2009) made recommendations more specific to this species. They also recommended thinning dense stands of ponderosa pine using uneven-aged management and retaining patches of tall large-diameter trees that are allowed to mature and become standing snags, and removing ground fuels from areas surrounding large snags prior to using prescribed fire (Solvesky and Chambers, 2009).

Allen's big-eared bats will use artificial roosts constructed to mimic exfoliating bark on snags in ponderosa pine forests (Chambers et al., 2002). Scent-detection dogs have been used to locate roost trees used by these bats (Chambers et al., 2015).

Macrotus californicus — California leaf-nosed bat (Family Phyllostomidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2010a, 2011b, 2017): Sensitive Species (Arizona, California, and Nevada state offices). U.S. Forest Service (2005a,b): Sensitive Species. International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G3, Vulnerable.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need. California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. Nevada Department of Wildlife (2013): Sensitive Mammal, Species of Conservation Priority. Nevada Department of Conservation and Natural Resources (2015a): Imperiled.

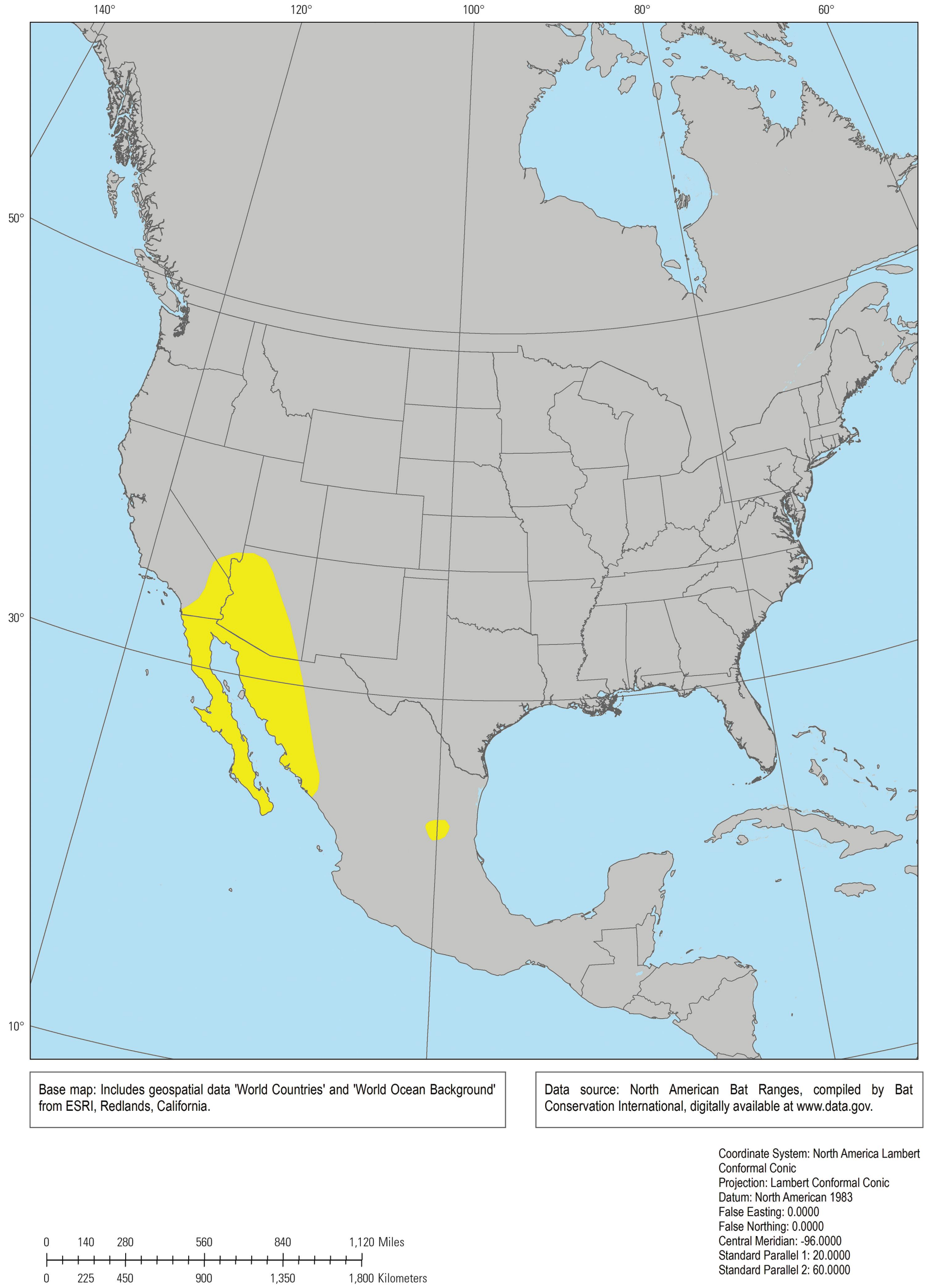
Description.— The California leaf-nosed bat (Fig. 19) is a medium-sized bat with an erect nose leaf, large ears, and large eyes. Unlike the three other leaf-nosed bats that regularly enter the lower southwestern U.S., the snout and tongue are short. The pelage appears gray, but the basal two-thirds of the hairs are white, with the upper third yellowish brown (Bradshaw 1961). Forearm lengths range 45 to 51 millimeters and body masses range 9.7 to 17.0 grams (Bradshaw, 1961).

Figure 19. California leaf-nosed bat, *Macrotus californicus* (photo by J. Scott Altenbach).

Distribution and Systematics.— This bat is the most northerly representative of the Family Phyllostomidae, the New World leaf-nosed bats, a group with over 140 species that is largely Neotropical in distribution. Unlike many other insectivorous bats of the U.S., the California leaf-nosed bat does not enter daily or seasonal cycles of torpor and is thus limited to warm regions and warm microclimates (Bell et al., 1986; see below). Currently there are two species recognized in the genus *Macrotus*. *M. californicus* is found in the deserts of southern California, southern Nevada, and southern Arizona in the U.S., southward through Baja California, most of Sonora, and northern Sinaloa, Mexico (Fig. 20); *M. waterhousii* occurs in tropical areas of southern and central Mexico and in islands of the Caribbean Sea.

Earlier literature can be confusing and may sometimes refer to populations of *M. californicus* in the southwestern U.S. as *M. waterhousii californicus* (if published at a time when only a single species with subspecies was recognized), whereas prior to the mid-1960s three species of *Macrotus* were thought to exist (Anderson and Nelson, 1965). Careful chromosomal, electrophoretic, and morphologic analysis showed that *M. californicus* is a species distinct from *M. waterhousii* (Davis and Baker, 1974; Greenbaum and Baker, 1976). Earlier taxonomic synonymies can be found in Grinnell (1918), Anderson and Nelson (1965), Anderson (1969), and Hall (1981). No subspecies of the California leaf-nosed bat are currently recognized. *Macrotus* is derived from Greek words meaning "long" and "ear". The specific epithet is based on geography. Other common names include California big-eared bat and Californian leaf-nosed bat.

Habitats and Relative Abundance.— California leaf-nosed bats are usually found in low desert habitats below about 1,100 meters (Bradshaw, 1961). Individuals do not range widely. The documented maximum distance for movement from a winter roost to a maternity colony was 93 kilometers, and the longest movement of any kind was 137 kilometers; the majority of recaptures



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 20. Approximate distribution of the California leaf-nosed bat, *Macrotus californicus*.

of banded individuals were near the site where they were originally banded (Cockrum et al., 1996). Surveys of regional bat faunas in mist nets set over water have seldom reported this species, perhaps because the bats are restricted in roosting and foraging habits, generally do not disperse far from roosts, and are maneuverable fliers that readily avoid capture (see below).

Arizona: California leaf-nosed bats occur primarily in Sonoran desert scrub in Arizona, where they probably do not make extensive seasonal movements to other habitats (Hoffmeister, 1986). In northwestern Arizona and adjacent areas, 1,667 of these bats were banded from 1959–1964 (Cockrum et al., 1996). Although large samples were banded at about nine roosts in western Arizona as noted above, they were not taken over water at multiple locations in the same region, despite captures of 3,458 individuals of 17 other species (Cockrum et al., 1996), nor during later mist netting or acoustic surveys (Brown and Berry, 1999). None were documented in the Arizona Strip of extreme northwestern Arizona despite previous records and 1,175 captures of 17 other species (Herder, 1998). At Kofa National Wildlife Refuge in southwestern Arizona, the California leaf-nosed bat ranked lowest in relative abundance of six species documented drinking at small artificial water sources in lower Colorado River Sonoran and Arizona Upland Sonoran desertscrub vegetation types, with 18 individuals captured among 427 bats (Rabe and Rosenstock, 2005). A major exception to rarity in surveys occurred after targeted mist netting for this species over four small artificial water sources in Sonoran desertscrub habitat at Cabeza Prieta National Wildlife Refuge in southwestern Arizona at the Mexican border, an area in close proximity to abandoned mines that housed colonies of this species (Schmidt, 1999). This was the most abundant species taken at this study area, with 470 bats captured among 1,153 bats of nine species documented on 68 nights of netting in all seasons during three calendar years (Schmidt, 1999).

California: Grinnell (1918:255) stated "In California, the leaf-nosed bat seems to be confined to the hottest parts of the Lower Sonoran zone, mainly on the Colorado Desert." Although somewhat more widespread in southern California in the past (Constantine, 1998a), habitats used by these bats in California are now limited to deserts in southeastern California, primarily in mountain ranges along the lower Colorado River (Brown, 2006). Natural history observations in California suggest that these bats utilize lower elevation desert habitats near preferred roosting sites in caves and abandoned mines, with foraging concentrated in desert washes and surrounding areas or over the river floodplain (Vaughan, 1959; Brown and Berry, 1991; Brown et al., 1993a,b).

Nevada: Differential use of habitat types within riparian areas in the Mojave Desert of southern Nevada by these bats was studied primarily using acoustic detections: California leaf-nosed bats occurred in each of four habitats (riparian marsh, mesquite bosque, riparian woodland, and riparian shrubland) about equally (Williams et al., 2006).

Foraging and Dietary Analysis.— These bats forage in desert habitats and seem to favor desert washes, at least during the warmer months, where they glean insects from riparian vegetation and the ground (Brown and Berry, 1991; Schmidt, 1999). Taking prey from the ground was first suggested by Hilda Grinnell (1918) who noted the capture of a California leaf-nosed bat in a mouse trap in 1908 and speculated that it was attracted to insects feeding on the bait. Banding and radio-tracking studies in the Cargo Muchacho Mountains of southeastern California have shown that in the area studied, these bats rarely travel more than five to ten kilometers from their roosts and forage primarily in desert washes where they were observed feeding on large moths and katydids (Brown et al., 1993a,b).

Vaughan (1959) described the flight of these bats as extremely maneuverable and rapid, but noted that while foraging their flight can be slow, buoyant, nearly silent, and will include hovering. Individuals watched while foraging flew within one meter of the ground, often dropping closer, and also foraged close to vegetation (Vaughan, 1959). Stomach contents of these bats taken in the

Riverside Mountains of California included many forms that were taken on the ground or from the surfaces of vegetation, including orthopterans (grasshoppers and crickets), noctuid moths and caterpillars, and scarab and carabid beetles (Vaughan, 1959); they will also alight on ceilings of grottos, caves, and abandoned mines to manipulate and consume larger prey items such as sphinx moths, grasshoppers, and beetles (Huey, 1925; Vaughan, 1959; Ross, 1964).

Ross (1964, 1967) examined 41 digestive tracts from individuals taken in both Arizona and in Mexico. Typical insect prey sizes ranged 40 to 60 millimeters and the bats primarily consumed the abdomens of the larger prey items. However, smaller items ranging down to 20 millimeters were also noted, including flying ants. As in California, prey included large slow-flying insects and mainly terrestrial species such as sphinx moths, short-horned and long-horned grasshoppers (Acrididae and Tettigoniidae), long-horned beetles (Cerambycidae), and caterpillars. Ross (1964) also reported that stomachs of these bats contained fruit or other vegetative matter, but these specimens were likely *M. waterhousii* taken in Mexico prior to a revised understanding of the systematics of *Macrotus*. Food items summarized from the literature by Bradshaw (1961) included coleopterans (Carabidae, Meloidae, and Scarabaeidae), orthopterans (including grasshoppers), lepidopterans (Sphingidae, Noctuidae, Cossidae, and caterpillars), odonates (dragonflies), homopterans (cicadas), dipterans, and hymenopterans. Other reports of prey include cockroaches and diurnal acridid grasshoppers and nymphalid butterflies (Bell et al., 1986), as well as small lizards (Brown, 2013). Many of these prey items were probably taken from the ground or surfaces of vegetation (Vaughan, 1959; Bradshaw, 1961; Bell, 1985).

California leaf-nosed bats have echolocation characteristics that are well suited for foraging in the cluttered situations encountered by species that glean prey from vegetation and ground surfaces (low intensity, high frequency, and short duration ultrasonic pulses), particularly in total darkness; they will also cue on audible sounds made by prey (Bell 1985). However, vision is very well developed compared to many other insectivorous bats, and they regularly interrupt echolocation and switch to vision to locate insects, particularly under moonlight conditions (Bell, 1985; Bell and Fenton, 1986).

Renal structure suggests that California leaf-nosed bats have good urine concentrating ability, consistent with their distribution in arid habitats, and they can persist in the laboratory for six weeks without access to drinking water (Lu and Bleier, 1981). Nonetheless, their maneuverability close to the ground also allows them to access small surface areas of water when available (Taylor, 2007). They regularly drink at such sources in southern Arizona, particularly females during lactation (Schmidt, 1999).

ROOSTING HABITS.— California leaf-nosed bats roost in abandoned mines and caves in the Desert Southwest, generally at elevations less than 762 meters (for example, Grinnell, 1918; Howell, 1920a; Brown et al., 1993a,b; Cockrum et al., 1996). Currently all known winter and maternity colonies in California are located in old mines, with the exceptions of two maternity colonies of 10 or fewer individuals in shallow caves (Brown, 2013). Most roosts reported from Arizona are in mines, although several caves are also used (Schmidt, 1999). This species has been characterized as an obligate user of abandoned mines in much of their range, and it has been suggested that their distribution may have expanded in response to the appearance of abandoned mines on the landscape (Bradshaw, 1961; Altenbach and Sherwin, 2002). Some caves and mines used as roosts are shared with several other species of bats (see for example, Bradshaw, 1961; Brown, 2013).

Winter Roosts: California leaf-nosed bats require warm roost temperatures of about 23 to 27ºC or higher and do not drop body temperatures to very low levels or hibernate (Bradshaw, 1961; Bradshaw, 1962; Bell et al., 1986; Brown and Berry, 1991). However, this species can be somewhat heterothermic during winter and can reduce body temperature to about 26ºC and appear lethargic within roosts (Bradshaw, 1961, 1962; Leitner and Ray, 1964). They also are capable of surviving somewhat lower body temperatures for short periods in laboratory experiments (Reeder and Cowles, 1951), but the thermoneutral zone (where increased metabolism is not required to maintain a stable body temperature) is limited to body temperatures of 33ºC and above (Bell et al., 1986). Using warm roosts in winter and minimizing energetic costs of echolocation appear to have allowed this species to extend its range farther north than any other bat in the mostly tropical Family Phyllostomidae (Bell et al., 1986).

Shallow caves that are suitable summer retreats may be abandoned seasonally in winter (Howell, 1920a), and in California these bats regularly use naturally geothermally warm abandoned mines during cold months (Bell et al., 1986; Brown et al., 1993a,b). Use of different mine tunnels during summer and winter also has been reported in northwestern Arizona (Cockrum et al., 1996). During winter in the California desert, where night-time temperatures can drop as low as 0ºC, they are known to form colonies (about 200 bats or more in size) in just a few geothermally heated desert mines and will switch among these sites if disturbed (Bell et al., 1986).

Fewer than 20 geothermally warm winter roosts were known in California, all in abandoned mines (Brown et al., 1993b). The largest currently known winter colony in the U.S. is in an abandoned mine on Bureau of Land Management lands in southeastern California, where counts of up to 5,000 have been made since 2002 (Brown, 2013). Winter counts during emergence at another mine on Bureau of Land Management property in Arizona were as high as 3,500 in 2002, but fluctuated among years (Brown, 2013). Recent winter emergence counts of over 2,000 bats have been documented at another long-occupied and now gated mine in southeastern California (Brown, 2013). In southwestern Arizona, one mine in the Trigo Mountains held about 1,500 to 2,000 California leaf-nosed bats in recent winters, with up to 3,500 estimated in 2002 (Brown, 2013). The largest winter colony size reported in mines in the Agua Dulce Mountains of extreme southern Arizona was about 500 bats (Schmidt, 1999). California leaf-nosed bats do not form dense clusters in winter (Brown, 2013).

Warm Season Roosts: Vaughan (1959) described daytime roosts of California leaf-nosed bats in caves, deserted mine tunnels, and grottos in the Riverside Mountains of southeastern California, where these bats occurred in groups of from just a few to 100 or more. They were usually within 9 to 24 meters of entrances and did not seem to require completely dark retreats. Most of the tunnels observed to harbor bats were from 1.5 to 2.0 meters high and wide and five to over 30 meters deep. Bats were not observed roosting in tight clusters, but small groups of up to 20 individuals were observed with each bat slightly separated from adjoining individuals (Vaughan, 1959; see also Cockrum et al., 1996).

Maternity colonies form during summer in mines or caves where temperatures reach 27–32ºC (Brown and Berry, 1991). Banding studies suggest life-long fidelity to roosts but also show that movement to alternate sites may occur when the bats are disturbed (Brown et al., 1993a,b). Roosts in the Arizona portions of the range are in habitats that usually do not reach temperatures as low as in parts of California, and some of these caves and mines may be occupied year-round, whereas others may function principally as summer or winter roosts (Hoffmeister, 1986; Schmidt, 1999). At a well-studied roost in an abandoned mine near Silverbell in southern Arizona the population of up to 350 individuals consisted of about half males and half females during March and April, but in summer months females segregated into maternity colonies and males broke into small groups (Bradshaw, 1961). From August through October, the sexes mixed again at the roost and mating took place, with an influx of bats seen in November during a presumed local migration; numbers declined during winter and only males were present (Bradshaw, 1961). Seasonal changes in colony sizes have been reported in mines in the Agua Dulce Mountains of extreme southern Arizona, with near equal adult sex ratios in some but with a preponderance of females in others (Schmidt, 1999). The largest warm season colony in the latter study was about 200–300 bats. Recent (2000–2013) maximum counts at the four largest known summer colonies in abandoned mines in the Lower Colorado River area of southeastern California and southwestern Arizona ranged from about 100 to 500 individuals, predominantly males, whereas counts in spring can be much higher and include females (Brown, 2013).

Night Roosts: These bats night roost in a wider variety of shelters than are used as daytime retreats (but may use diurnal retreats for night roosting as well). California leaf-nosed bats tend to begin appearing in night roosts about two hours after emergence and often join other conspecifics, followed by additional foraging bouts prior to returning to the diurnal roost (Vaughan, 1959; Bradshaw, 1961; Bell et al., 1986). They have occasionally been reported to night roost in buildings and bridges, where they hang up to manipulate prey and digest their early evening meals at temperatures warmer than ambient (for example, Grinnell, 1914; Hatfield, 1937; Vaughan, 1959; Brown, 2013).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Stephens (1906) reported a high incidence of twinning in California leaf-nosed bats but gave no details. Subsequent observations show that twinning can occur but is very infrequent (Bleier, 1975a,b). "Nearly every one" of 61 adult females captured in a cave with a colony of 300 in Riverside County, California in April 1908 had a single embryo, and "none was found to contain more" (Grinnell, 1918:257). Cockrum (1955) summarized records of seven other females, six with one embryo and one with two. Bradshaw (1961) reported only single embryos in 175 cases from Arizona. Five females from Baja California, Mexico also had single embryos (Jones et al., 1965). Young are born around June, following fertilization in autumn and a long period of delayed development with an embryonic diapause of over four months (Bradshaw, 1961, 1962; Bodley, 1974; Bleier, 1975a,b). Sex ratios of young are 1:1 (Bradshaw, 1961).

Females mate in their first autumn, but males do not (Bradshaw, 1961; Krutzsch et al., 1976). Some of the above natural history observations on litter size suggest that natality is high, although all such observations stem from captures at maternity roosts. Huey (1925) reported all of 12 females taken at a maternity colony in a mine during May 1924 were pregnant. One study found that 95% of 188 females taken in mist nets over water in southern Arizona during the maternity season were reproductive, although the great majority of these were lactating and thus had greater water needs (Schmidt, 1999), perhaps adding a positive bias. Nonetheless, this result was identical to the simultaneous finding that 95% of 268 females taken at maternity roosts in the nearby Agua Dulce Mountains also were reproductive (Schmidt, 1999). We are unaware of any published literature with quantitative data concerning inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Mortality due to vandalism has been recorded, including the killing of 120 California leaf-nosed bats by teen-aged boys in an old mine (later permanently sealed; O'Farrell, 1970) near Las Vegas, Nevada during winter 1928 (Burt, 1934). Much more recent killing has been reported at mines monitored along the Lower Colorado River in California and Arizona (Brown, 2013).

This species may be more susceptible to accidental mortality (such as ensnarement on spines of desert plants; Stager, 1943a) than other species of bats because of their habit of foraging close to the ground. Possible predators include skunks and owls (Bradshaw and Hayward, 1960; Bradshaw, 1961). Deaths due to rabies have been documented (Constantine, 1979). They have been sampled for persistent chemical contaminants, with some chemicals causing concern but without documentation of associated mortality or effects on reproduction (King et al., 2001, 2003; see

"Management Practices and Concerns" below). A maximum life span of about 15 years has been reported from banding studies (Brown et al., 1993a,b).

Population Trend: Counts at five colonies in Arizona were analyzed for temporal trends but none was detected (Ellison et al., 2003). Internal counts at one mine were found to vary greatly across multiple visits both within and among seasons, showing the difficulties of attempting to determine trends in count data for this species (Ellison et al., 2003). Emergence counts of these bats also can be influenced by strong negative effects of observation method (for example, human observers or video recording), the presence of other bat species in the same roost, bright moonlight, very cold weather, and wind (Brown, 2013).

Historical accounts suggest much greater past abundance of California leaf-nosed bats than known at present. For example, Howell (1920a:172), remarked that of the many caves along the rocky coastline of the Salton Sea "nearly all are tenanted by colonies of this bat—from a score to two-hundred individuals to a colony." These and other historically known colony sites are apparently now abandoned, and other more recently documented colonies have been abandoned or have declined (Brown, 2013). As examples, Brown and Berry (1991) reported the sealing of a maternity colony site in California during open pit mining operations, as well as the decline of a winter roost population that was stable at 150 animals in 1976 to 11 bats by 1990. This reduction was attributed to destruction of desert wash vegetation as foraging habitat and disturbance during resumed mining (Brown et al., 1993a,b; Brown, 1995). Constantine (1998a) reported the absence of this species from two caves in southern California that had housed low numbers in the 1940s (one cave had been destroyed, the other had signs of use as a "party site" and was surrounded by housing developments; Brown and Berry, 2005:14). A mine shaft used by a colony in Nevada was flooded by the impoundment of the Colorado River to form Lake Mead (O'Farrell, 1970), with unknown population consequences, and a mine tunnel in Arizona that formerly housed these bats was sealed shut (Brown, 2013).

Recent multi-agency sponsored monitoring of California leaf-nosed bat colonies along the Lower Colorado River from Laughlin, Nevada to near Yuma, Arizona began in 2002, and was initially based on emergence counts at ten mine complexes (Brown, 2013). Counts were made through 2010, with 6 of the mines also having prior data available and three more mines added after 2010. Counts at all but one mine showed year-to-year variability but no discernible trends (Brown, 2013). Counts at one ungated mine on the Imperial National Wildlife Refuge in Arizona used as a maternity colony declined from over 700 bats in spring 2001 to less than 100 in spring 2013, likely due to visitor disturbance (Brown, 2013). Emergence counts during winter at a long-occupied and now gated mine in California have appeared stable at over 2,000 bats during monitoring from 2001 to 2013 (Brown, 2013).

Population Genetics: Estimates of mean heterozygosity based on allozyme variation at 17 loci in a sample of 45 individuals from a mine in Pima County Arizona were quite low (0.03), indicating low genetic variability in that sample (Straney et al., 1976).

Management Practices and Concerns.— Creation and abandonment of mines in the western United States over the last two centuries could have initially added roosting habitat for these and other cavernicolous bats. However, some of these possible gains are subsequently lost as abandoned mines begin to naturally fill or are closed for safety reasons. California leaf-nosed bats will roost in mines fitted with bat-compatible gates and, as noted in the following examples, properly designed and installed gates are an effective way of protecting this species from human disturbance. The National Park Service has used bat-compatible closure methods at abandoned mines occupied by this species at Lake Mead National Recreation Area and Joshua Tree National Park (Burghardt, 2000). An abandoned mine on Bureau of Land Management property in southeastern California housing a wintering colony of about 2,000 of these bats has been successfully gated, resulting in increased use by bats (Henry, 2002), as has another mine in the area that was gated in 2006 (Brown, 2013). In Arizona, a wintering colony of about 400 individuals in an abandoned mine being encroached upon by suburban sprawl near Phoenix has also been protected with bat-friendly gating (Corbett, 2008), as has a mine in the Trigo Mountains of the Lower Colorado River area that continues to serve as both a winter roost and a lek mating area in autumn since gating in 2007 (Brown, 2013). In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that California leaf-nosed bats continued using gated mines over the long-term, tolerated various gate designs, and that the landscape location and structural complexity of a mine were better predictors than gate characteristics in determining if this species would continue using a site after gating.

California leaf-nosed bats will drink from artificial water sources provided in arid areas, but whether addition or removal of such water sources influences local populations remains unknown (Schmidt, 1999).

King et al. (2001) reported on concentrations of potentially toxic elements and organochlorines in small numbers of bats sampled at two sites in Arizona (four samples for organochlorines) and California (five samples analyzed for organochlorines, six for metals) in 1998. None of the bats had concentrations of toxic elements indicative of harmful effects, and organochlorines were present only at very low concentrations. However, King et al. (2003) analyzed a larger sample of individuals at former mine sites on the Kofa National Wildlife Refuge in 2001 and 2002, including two abandoned lead mines. They reported lead in carcasses and livers of these bats from the former lead mines at exceptionally high concentrations but were unable to directly link these high concentrations with impacts on the health of the bats. King et al. (2003) also found very high lead levels in the soils from the floor of these mines and hypothesized that the leaf-nosed bats were accumulating lead though grooming lead particles from dust on the fur and from inhaling lead-contaminated dust within the mines. The analyses in this study also included up to 17 other toxic elements, but concentrations of these other elements were not considered to be elevated.

Notes and Comments.— Natural history observations by Dr. Patricia Brown and colleagues strongly indicated that California leaf-nosed bats have a lek-based mating system: multiple males were seen to hang singly from small chambers in the ceilings of a mine, singing and displaying and chasing away other males, while females chose certain of these males for mating (Anonymous, 1995).

Myotis austroriparius — Southeastern myotis (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G4, Apparently Secure.

State Designations: Alabama Department of Conservation and Natural Resources (2015a,b): Priority 1 Species of Greatest Conservation Need, Highest Conservation Concern. Arkansas Game and Fish Commission (Fowler, 2015): Species of Greatest Conservation Need. Florida Fish and Wildlife Conservation Commission (2012): Species of Greatest Conservation Need. Georgia Department of Natural Resources (2015): High Priority Species. Illinois Department of Natural Resources (2015): State Endangered. Indiana Department of Natural Resources (2006, 2015): Special Concern, Species of Greatest Conservation Need. Kentucky Department of Fish and Wildlife Resources (2013): Species of Greatest Conservation Need. Louisiana Department of Wildlife and

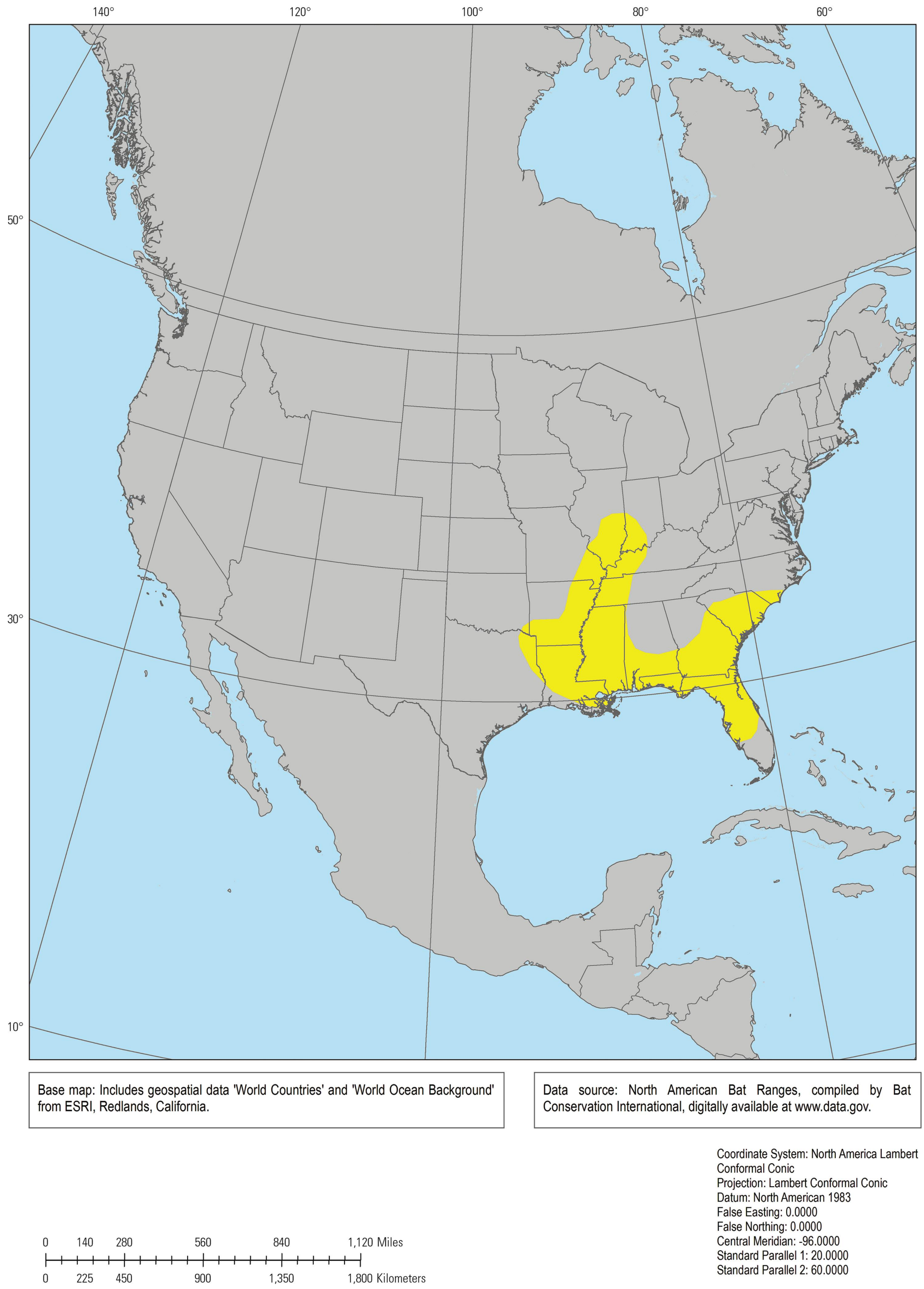
Fisheries (2015): Tier II Species of Greatest Conservation Need. Maryland Department of Natural Resources (2005, 2016): Species of Greatest Conservation Need. Mississippi Department of Wildlife, Fisheries and Parks (2005, 2015): Species of Greatest Conservation Need. Missouri Department of Conservation (2016): Species of Conservation Concern, Critically Imperiled. North Carolina Wildlife Resources Commission (2014): Special Concern Species. Oklahoma Department of Wildlife Conservation (2005, 2016): Species of Greatest Conservation Need Tier I, II. South Carolina Department of Natural Resources (2005, 2015): Highest Priority Species of Greatest Conservation Need. Tennessee Wildlife Resources Agency (2005, 2015): Tier I Species of Greatest Conservation Need. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need. Virginia Department of Game and Inland Fisheries (2005, 2015b): Tier IV Species of Greatest Conservation Need.

Description.— The pelage of the southeastern myotis (Fig. 21) has been described as somewhat wooly, with little or no contrast in color from the base to the tips of the hairs; coloration is variable, ranging from gray to orange or russet above and tan to white ventrally, with females generally more brightly colored than males (Jones and Manning, 1989; Humphrey and Gore, 1992). Forearm lengths of adults ranged 36 to 42 millimeters in a sample of 29 females and 11 males from Florida, with adult body masses in April-May ranging 5.4 to 10.4 grams in 28 females (large embryo weights subtracted) and 5.4 to 6.6 grams in 11 males (Sherman, 1930). Individuals from Indiana ranged 4.1 to 9.2 grams in a sample of 27 males and 5.1 to 9.1 grams in 16 females (Mumford and Whitaker, 1982). The southeastern myotis lacks a keel on the calcar.

Figure 21. Southeastern myotis, *Myotis austroriparius* (photo by J. Scott Altenbach).

Distribution and Systematics.— The geographic range (Fig. 22) extends from the northern half of peninsular Florida to southeastern Virginia and Maryland on the Atlantic Coast, westward from the Atlantic Coast through North Carolina, South Carolina, Georgia, Alabama, Mississippi and Louisiana to eastern Texas and southeastern Oklahoma, and from southern Arkansas through the Mississippi River and Ohio River valley areas of southeastern Missouri, western Tennessee, and Kentucky northward to southernmost Illinois and southern Indiana (LaVal, 1967; Jones and Manning, 1989; Amelon et al., 2006; Lacki and Bayless, 2013). There are no subspecies of *Myotis austroriparius*, and previously applied subspecific designations are no longer recognized (LaVal, 1970). Jones and Manning (1989) provided a taxonomic synonymy of past scientific names applied to the southeastern myotis. The generic name originates with Greek words meaning "mouse" and "ear". The specific epithet is from Latin words meaning "southern" and "of a river bank". Other English common names for this species include southeastern bat, southeastern brown bat, Mississippi myotis, and Mississippi bat.

Habitats and Relative Abundance.— Southeastern myotis are often found near water (Rice, 1957), and can be most abundant in bottomland hardwood forests, but also can be found in upland habitats (LaVal, 1970). Bat community surveys in southeastern pine forests typically yield low relative abundances of southeastern myotis. They compose generally nine percent or fewer of



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 22. Approximate distribution of the southeastern myotis, *Myotis austroriparius*.

total captures in mist net surveys or total acoustic detections of all identifiable species of bats in pine forests (reviewed by Debelica-Lee and Wilkins, 2014). Habitat occupancy modeling based on acoustic detections in managed pine forests was analyzed in six southern states (Bender et al., 2015). Within such habitats *M. austroriparius* was more likely to be found at sites with a higher proportion of stands greater than 30 years old and lower vegetative clutter, perhaps because these sites were also more likely to include trees suitable for roosting; over all study areas, this species ranked fifth out of the six most commonly detected species (Bender et al., 2015).

Arkansas: In northeastern Arkansas, individuals captured while foraging or traveling were no more likely to be captured over land than over water (Medlin and Risch, 2008). They were the third most abundant species of bat in mist-netting surveys in six wildlife management areas and national wildlife refuges in northeastern Arkansas bottomland hardwood forests (62 individuals among 302 bats of eight species; Medlin and Risch, 2008). Southeastern myotis were the most abundant species (268 captures among 556 bats of eight species) at 35 sites surveyed during summers 1997–1999 in bottomland hardwood forest of the Rex Hancock/Black Swamp Wildlife Management Area of eastern Arkansas (Hoffman, 1999).

Florida: The largest populations of southeastern myotis are thought to occur in Florida (Amelon et al., 2006). Foraging individuals were the second most commonly detected species among seven that were identifiable by echolocation activity in longleaf pine habitat in Florida sandhills subject to a variety of prescribed burn schedules (Armitage and Ober, 2012).

Illinois: These bats ranked low in relative abundance in mist-net surveys over water in various habitats within southern Illinois, where 68 were captured among 474 bats of 12 species, biased by 63 taken in a foraging area utilized by a nearby maternity colony (Gardner et al., 1992; Hofmann et al., 1999).

Louisiana and Mississippi: This was the second most abundant species in surveys of bottomland hardwood forests in northeastern Louisiana (48 bats among 112 bats of four species; Rice, 2009). They ranked fourth in relative abundance (39 southeastern myotis captured among 419 bats of seven species) in extensive mist-net surveys conducted on 113 nights at 79 sites in nine study areas across Mississippi during 2002–2006, and were captured at six study areas in habitats characterized as bottomland hardwood forests, mixed hardwood forests, upland mixed hardwood forests, and swamp forest (McCartney, 2007). A second mist-netting survey in summer 2007 focused on four refuges within the Theodore Roosevelt National Wildlife Refuge complex in western central Mississippi, with 28 nights of netting at 23 sites (McCartney and McCartney, 2008). Southeastern myotis ranked second in relative abundance (47 captured among 201 bats of 5 species) across all four refuges and were primarily found in bottomland hardwood forest habitat (McCartney and McCartney, 2008). In contrast, in managed loblolly pine forests of eastern Mississippi only one southeastern myotis was taken in mist net surveys that yielded 284 bats of 6 species (Miller, 2003).

North Carolina and South Carolina: Southeastern myotis ranked fourth in relative abundance (42 captured among 452 individuals of eight species) netted around water and at corridors within forests on the Coastal Plain of North Carolina during summer (Grider et al., 2016). Acoustic sampling in South Carolina showed that Carolina bay wetlands (pond habitats in Coastal Plain depressions) that had been ditched and drained showed greater echolocation activity of this species in comparison with interior upland pine-hardwood forest (Menzel et al., 2005). The species was detected most often in association with intact Carolina bay habitat and were more likely to be present in bottomland habitats rather than upland habitats and pine communities, highlighting the potential importance of such habitats to the species in this region (Ford et al., 2006). Menzel et al. (2003) examined documented records of all species of bats across the four physiographic provinces of South Carolina based on 1,002 museum specimens and reports of 2,002 bats captured during surveys. They were found in the lower Piedmont, Upper and Lower Coastal Plain provinces, and ranked third lowest in numbers of specimens (7) and fifth lowest in survey captures (22) among 14 species documented in the state. In Georgia, they are only known from two of the six physiographic provinces, the Upper Coastal Plain and Lower Coastal Plain, but they rank intermediate in relative abundance (114 records) among 1,222 combined museum and capture records of bats of 16 species compiled for the state (Menzel et al., 2000).

Tennessee: This was the second most abundant species (91 captures among approximately 250 individuals of 12 species) captured in mist nets over water in western Tennessee, with most captured over streams in bottomland hardwood forest (Graves and Harvey, 1974). In mist-net surveys over water in riparian areas within mixed human-modified landscapes (including managed oak-hickory forests, agricultural fields, and pastures) of western Tennessee, these bats were the least captured (nine bats) among 220 individuals of four species (Gilley and Kennedy, 2010).

Texas: In predominantly loblolly pine forests of southeastern Texas, southeastern myotis ranked fifth in relative abundance (21 bats) among 382 individuals of eight species captured in mist nets over water (Debelica-Lee and Wilkins, 2014).

Foraging and Dietary Analysis.— Southeastern myotis feed close to the surfaces of streams, ponds, and lakes and low over open fields (Rice, 1957). In dry uplands of Florida, these bats are reported to feed around live oaks (Humphrey and Gore, 1992). Those radio tracked in southern Illinois were inferred to forage over floodplains and in mature forested wetlands, ranging about six kilometers from capture sites and nine kilometers from the nearest known roost (Gardner et al., 1992; Hofmann et al., 1999). Prey in Florida includes mosquitoes, small beetles, crane flies, other aquatic insects, and moths (Zinn and Humphrey, 1981). Fecal pellets from 10 individuals sampled in southern Illinois contained about 60% caddisflies (Trichoptera) followed by hemipterans, lepidopterans, and dipterans, with almost no coleopterans (Feldhamer et al., 2009). These bats have been described as late feeders, emerging from cave roosts well after sunset (Rice, 1957).

Roosting Habits.— In Florida, caves are important roosting sites for this species at critical times of the year (Rice, 1957). Movements of up to 43 kilometers between caves have been documented through banding (Rice, 1957). These bats sometimes roost in association with other species of bats, including Brazilian free-tailed bats (*Tadarida brasiliensis*), little brown myotis (*Myotis lucifugus*), gray bats (*Myotis grisescens*), tricolored bats (*Perimyotis subflavus*), and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), as summarized by Jones and Manning (1989) and Jennings and Layne (1957).

Although caves are typical roosting sites in karst regions, elsewhere southeastern myotis also roost in hollow trees, culverts, bridges, abandoned mine shafts, and buildings, and will occupy such roosts in parts of the distribution that lack caves (Davis et al., 1955; Rice, 1957; Lowery, 1974; Heath et al., 1986; Walker et al., 1986; McDonnell, 2001; Clark, 2003; Felts and Webster, 2003; McCartney, 2007). Maternity colonies ranging up to several thousand adults also have been known to form in buildings in regions that include caves (Sherman, 1930; Hermanson and Wilkins, 1986; McCartney, 2007).

Colonies of several hundred adults have been observed roosting in concrete bridges in Florida (Gore and Studenroth, 2005). Solitary individuals roost under bridges during late summer and autumn in Louisiana (Lance et al., 2001), and small numbers are known to use concrete box culverts in eastern Texas throughout the year (Walker et al., 1986). One culvert in Mississippi was used as a maternity colony by several hundred southeastern myotis, with other culverts only known to house solitary bats; three cisterns in Mississippi each held maternity colonies of about 5,500 to 6,500 southeastern myotis and also housed from several hundred to over 1,500 bats during winter

(McCartney, 2007). McDonnell (2001) surveyed 990 bridges and culverts for use by bats in the Coastal Plain of North Carolina during summers 1997 and 1998 and found only 12 used as roosts by southeastern myotis, 11 housing solitary bats and one with seven bats; all were in swamp or bottomland hardwood forest habitats. Southeastern myotis were not found roosting under concrete slab bridges, I-beam bridges, steel multi-beam bridges, or steel pipe culverts, but they used channel beam bridges, timber multi-beam bridges, T-beam bridges, and one concrete box culvert (McDonnell, 2001).

Relatively little was known about the tree-roosting habits of this species until recently (Barclay and Kurta, 2007). Species of trees in which hollows have been used as roosts include black mangrove (*Avicennia nitida*; Rice, 1957), bald cypress (*Taxodium distichum*), American beech (*Fagus grandifolia*), eastern cottonwood (*Populus deltoides*), water tupelo (*Nyssa aquatica*), black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), white oak (*Quercus alba*), sweetgum (*Liquidambar styraciflua*), American sycamore (*Platanus occidentalis*), and ash (*Fraxinus* sp.) (Whitaker and Hamilton, 1998; Hoffman, 1999; Clark, 2003; Gooding and Langford, 2004; Mirowsky et al., 2004; Carver and Ashley, 2008; Rice, 2009; Clement and Castleberry, 2013a; Fleming et al., 2013a; Stuemke et al., 2014). Southeastern myotis broadly overlap in habitat type with Rafinesque's big-eared bats, but there is evidence that in some areas they may choose roosts in hollow trees with dissimilar characteristics to those used by Rafinesque's big-eared bats (Stevenson, 2008; Trousdale, 2011).

Trees used as roosts in bottomland hardwood forests at Noxubee National Wildlife Refuge in Mississippi had greater girth, greater cavity widths, lower cavity heights, and larger internal chambers than trees that had no evidence of use, but tree species and sizes were chosen randomly (Stevenson, 2008; see below for additional information on roosts in trees). In eastern Texas, transect searches and radio tracking of three southeastern myotis showed that stands where roost trees were located were in areas with higher densities of smaller trees than stands supporting Rafinesque's big-eared bats, but other aspects of roost trees did not differ between roosts used by the two species (Stuemke et al., 2014). However, compared to trees that were unused, roost trees used by both species were larger, had larger diameters and cavities, greater numbers of entrances, were in trees with entrances higher above ground, and were located in stands with higher numbers of large trees (Stuemke et al., 2014). In eastern Arkansas, two radio-tracked female southeastern myotis roosted with 32–104 conspecifics in two hollow, live water tupelo trees with large, triangular basal openings and enclosed ceilings (Hoffman, 1999).

Winter Roosts: In the southern part of the distribution, southeastern myotis remain active throughout much of the winter (Humphrey and Gore, 1992) and are seldom found torpid except for brief periods (Lowery, 1974; Jones and Pagels, 1968). In northern parts of the range, in contrast, caves appear to be essential for winter hibernation. In southern Indiana, southeastern myotis have been found hibernating in caves during seven months of the year, and hibernation lasts four to five months in northwestern Florida caves (Rice, 1957). Hibernating colonies as large as 3,000 bats were reported from caves in western Kentucky (Harvey et al., 1991). Caves utilized in winter can be different from those used during warm seasons, and during winter they may be more concentrated in fewer caves than utilized in summer (Humphrey and Gore, 1992). Up to 150 individuals were found hibernating in abandoned mines and old water wells in Arkansas (Davis et al., 1955; Heath et al., 1986; Saugey et al., 1989, 1993).

During winter in peninsular Florida these bats do not usually undergo deep hibernation (but will do so in other parts of their range, and can become torpid during strong cold spells even in Florida). Although small numbers can be found in peninsular Florida caves during winter, many instead roost in small groups or as individuals in hollow trees and other structures (including buildings and houses), and bats often roost near or over water within bridges, culverts, storm drains, and boat sheds (Rice, 1957; Bain, 1981; Felts and Webster, 2003). These bats will shift to warmer roosts in buildings during cold snaps in Florida (Bain, 1981).

Southeastern myotis also will roost in hollow trees during winter in the southern parts of the distribution that lack caves. Two males radio tracked in winter in Georgia switched roosts in trees every 2.8 days with distances between successive roosts ranging from 15 to 2,237 meters (Clement and Castleberry, 2013b). Trees used as roosts in winter were smaller and had smaller but higher roost openings than trees used in summer, perhaps to avoid trees with entrances subject to winter flooding. As during summer, bats did not use trees with chimney-like openings at the top; winter roosts were in hardwood forest with lower flooding than the cypress-gum swamps used in summer (Clement and Castleberry, 2013a,b). The seasonal differences in tree roosts found in the Georgia study indicate that in some areas findings from summer studies alone may not reveal a full suite of roost attributes necessary for year-round management (Clement and Castleberry, 2013b).

In eastern Mississippi, trees with cavities used by southeastern myotis in winter had larger girths and larger cavity volumes than trees with cavities that were unoccupied, but in spring, trees that were selected were similar in girth and cavity size (Fleming et al., 2013a). On the landscape scale, roost trees found in winter during the eastern Mississippi study were at lower elevations, and during spring they were farther from roads than unoccupied trees with cavities (Fleming et al., 2013a). Availability of water in winter was a possibly important landscape characteristic for this species at Noxubee National Wildlife Refuge in Mississippi, where colony sizes in both winter and summer were 50 or fewer bats and larger trees were used as winter roosts than were used as summer roosts (Stevenson, 2008). As in summer, only water tupelo trees with basal hollows and no upper openings were observed to be used by individuals during winter at Upper Ouachita National Wildlife Refuge in northeastern Louisiana, with some individual trees used much more frequently than other roost trees (Rice, 2009). Most winter observations were of solitary bats; larger roosting groups in winter were often inactive, but left roosts to forage on warmer days (Rice, 2009).

Warm Season Roosts in Caves: In Florida, caves used by maternity colonies often have permanent water and large areas of horizontal ceilings at least 2 meters above the water surface (Rice, 1957; but see below). Although clusters of these bats have been observed in dry areas in some caves (Mumford and Whitaker, 1982; Gore and Hovis, 1994), colonies in caves are often found over water, a roosting habit which may deter predators as well as increase humidity for the clusters of developing young (Rice, 1957; Foster et al., 1978). Banding returns in Florida caves suggest that adults have a strong fidelity to specific caves, but that juveniles are more likely to wander (Rice, 1957). Many caves used as nursery sites in Florida have large, horizontal high ceilings as well as permanent bodies of water, and bats may desert caves when the water level is low (Rice, 1957; Bain, 1981). However, there is conflicting evidence for the importance of over-water roosts for this species, and additional study of this topic is desirable (Gore and Hovis, 1994).

Maternity colonies of southeastern myotis numbering from about 2,000 to 90,000 adults form in dense clusters (1,600 per square meter) in Florida caves during late March and early April (Rice, 1957). Young are born from late April to late May, with young bats taking flight at five to six weeks of age; adult males join maternity colonies in large numbers after this time, with most bats dispersing from these sites in October (Rice, 1957). A colony of about 1,000 southeastern myotis utilized a cave in Mississippi when visited in both July and October (McCartney, 2007).

Warm Season Roosts in Trees: Colonies in trees include maternity groups but tend to be smaller than those found in other structures (Clark, 2003; Mirowsky et al., 2004). A count of 101 bats was reported from a hollow water tupelo in southern Illinois (Gardner et al., 1992; Hofmann et al., 1999). Roost trees utilized by southeastern myotis maternity colonies in bottomland forests will be abandoned during periods of unusually high flood waters (Gardner et al., 1992; Hofmann et al., 1999).

A multi-site roost selection study on the coastal plain of Georgia searched 1,731 hollow trees on transects and 22 roosts were found (1.3%), with three the maximum number of bats seen in a roost (Clement and Castleberry, 2013a). Tree characteristics suggested that microclimates of favored trees were a likely factor in their selection. Tree selection by this species in summer included species (water tupelo was nearly always selected), solid wood volume (larger trees favored), and lower canopy cover; however, there was a strong site effect, with most sites found in areas with a karst substrate and nearby caves also known to be used by this species (Clement and Castleberry, 2013a). Transect surveys at three study areas with appropriate habitat in South Carolina yielded 361 trees with cavities, with 12 (3.3%) found to be used as roosts by these bats (Loeb, 2017). Only water tupelo trees were observed to be used by this species during summer at Upper Ouachita National Wildlife Refuge in northeastern Louisiana, with some individual trees used much more frequently than other roost trees (Rice, 2009). Colony sizes varied in the Louisiana study, with groups of one to ten bats seen most frequently, but with colony sizes of up to about 300 bats observed; only trees with basal hollows and no upper openings were used as roosts, and only the ceilings or upper parts of tree cavities were occupied (Rice, 2009).

In western Tennessee, five southeastern myotis were radio tracked during summer to eight roost trees at Pinson Mounds State Archaeological Park; the bats roosted in living hollow water tupelo trees which did not differ in size from potential trees that were unused, but were smaller than hollow trees used by sympatric Rafinesque's big-eared bats (Carver and Ashley, 2008).

Population Ecology.— Litter Size, Natality, and Female Reproduction: This is the only species of *Myotis* in North America that regularly gives birth to twins. Twenty of 28 females (71%) at a maternity colony in a Florida attic had twin embryos or young and the remainder had singletons (Sherman, 1930). Over 90% of the litters of 1,489 pregnant females subsequently observed in Florida consisted of twins for a mean litter size of 1.9 young per female (Rice, 1957). A rare case of triplets has also been documented (Foster et al., 1978). Parturition and lactation take place in spring and summer; descriptions of parturition including births of twins were provided by Sherman (1930). Sex ratios of newborn are 1:1 based on examination of 2,847 young bats in Florida (Rice, 1957).

Sexual maturity in females is reached as yearlings in peninsular Florida, based on subsequent recaptures at a maternity roost of 46 female bats banded as juveniles that were all pregnant at age one year (Rice, 1957). A sample of 153 females older than one year from the same maternity roost were all pregnant (Rice, 1957). Estimated natality based on females captured away from maternity colonies is mostly unavailable but was 100% in a sample of 10 adult females captured over water in eastern Texas (Debelica-Lee and Wilkins, 2014), 50% in 16 females netted away from roosts in Arkansas (Fokidis et al., 2005), and 93% in 41 females captured in southern Illinois near a maternity roost (Hofmann et al., 1999). Non-reproductive females may roost apart from maternity colonies (Hermanson and Wilkins, 1986).

Survival: No modern data exist on adult survival rates (Gore and Hovis, 1994), although crude estimates on proportion returning annually were provided by Rice (1957). Based on a very simple model, Rice (1957) suggested that in order for populations to remain stable in Florida, an annual survival of at least 46% was necessary; more recent analyses for other species of temperate zone bats suggest this estimate may be too low for stability (for example, species reviewed in O'Shea et al., 2011c), but these other species have smaller litter sizes. Modern population dynamics simulations have not been published. Survival to weaning at a roost in Florida was estimated at 88.2% (Foster et al., 1978). Maximum longevity is at least 6 years (Paradiso and Greenhall, 1967).

Mortality Factors: Young are born at earlier stages of development than in many other species of bats, and as a consequence pre-weaning mortality (sometimes from falling into water beneath roosts) is high at 11.8% and is most severe shortly after birth, with multiple carcasses of immature bats observed under roosts (Foster et al., 1978; Hermanson and Wilkins, 1986). Adult mortality may also be high where prolonged hibernation does not occur because of greater exposure to various risks during the course of being active a large number of days of the year; twinning with altricial young may have been selected for as a natural demographic compensation for higher mortality (Foster et al., 1978; Humphrey and Gore, 1992).

Records on predation of adults and young by snakes, owls, and opossums (*Didelphis virginianus*) have been summarized by Jones and Manning (1989), Humphrey and Gore (1992), and Lacki and Bayless (2013). Rice (1957) found 42 carcass remains taken by unspecified owls at the mouth of one cave and also suggested that cockroaches are important predators on fallen nonvolant young. Foster et al. (1978) found two yellow rat snakes (*Pantherophis alleghaniensis*) beneath a colony in a house with combined remains of 11 southeastern myotis (including adults) in their digestive tracts.

DNA from the fungus causing white-nose syndrome was reported for the southeastern myotis since the early years of the epizootic (Foley et al., 2011). Clinical disease was confirmed in an individual southeastern myotis sampled in Alabama during the winter of 2016/2017 (Alabama Department of Conservation and Natural Resources, 2017), but major mortality from this disease has not yet been reported in this species. Fatal rabies infections occur in this species (for example, Richardson et al., 1966; Bigler et al., 1975; Constantine, 1979; Streicker et al., 2010), but the prevalence can be low: one rabies-positive bat was found out of 1,998 southeastern myotis shot in flight in Florida during the 1950s (Schneider et al., 1957). These bats are usually infected with a rabies virus variant that is species-specific (Streicker et al., 2010). No mortality has been associated with macroparasites (species listed in Rice, 1957; Whitaker and Wilson, 1974; Jones and Manning, 1989).

Flooding can cause catastrophic mortality in southeastern myotis. Carcasses of at least 6,500 of these bats were observed awash in one Florida cave in 1989 following flooding from a summer downpour, and an estimated 57,000 were killed in a second cave flooded by the Apalachicola River during record high water in 1990 (Gore and Hovis, 1994). Flooding in 1994 killed 85,000 bats in Snead's Cave, Florida (Whitaker and Hamilton, 1998). Entrapment of colonies in hollow trees during flooding of bottomland hardwood forests has been observed over the short term (Rice, 2009), and because these bats seem to prefer hollow trees with no upper openings (see "Roosting habits" above), extended submergence of basal openings may also cause mortality.

Encroachment of human populations in areas where southeastern myotis aggregate in caves has resulted in mortality due to vandalism and deliberate destruction (see "Management Practices and Concerns" below). The only detailed study on contaminants in this species focused on toxic elements near an industrial source in northern Florida; concentrations of cadmium were higher in kidneys and livers but not at levels indicative of mortality (Clark et al., 1986).

Population Trend: Ellison et al. (2003) compiled data from six colonies across the range that had time series of counts on at least four separate years. Five showed no consistent trend and one declined based on non-parametric analyses: the maternity colony at Sweet Gum Cave in Florida dropped from 64,000 adults (listed in Ellison et al., 2003 as containing 170,000 bats, but that value included young) in 1936 to zero in 1991. Some of this decline was attributed to a cave passage being blocked by rock collapse and modifications to the cave entrance by the land owner (Rice, 1957; Gore and Hovis, 1994). Anecdotal accounts and historical appraisals of status, however, also generally indicate declines. Barbour and Davis (1969) suggested that the population in the lower Ohio River Valley was rare compared to the past and possibly close to extinction; the species is considered uncommon or rare in the northernmost states within its range (Barbour and Davis, 1974; Hoffmeister, 1989; Sealander and Heidt, 1990). According to Mumford and Whitaker (1982), wintering populations in these areas decreased substantially since 1949. In southern Illinois, a search of 52 suitable caves and mines during winter in 1982–1991 revealed just one inhabited by southeastern myotis (Gardner et al., 1992). This site showed a range of counts among winter visits of from two to 220 hibernating individuals, with the bats seeming easy to arouse. Two sites with larger numbers (90–120 and 120) of hibernating bats in the past were no longer used or suitable due to vandalism or modification (Gardner et al., 1992).

The first documented locality for this species in Arkansas was a mine drift in the Ouachita Mountains that was subsequently inundated by an impoundment (Davis et al., 1955); a second locality discovered in the Ouachita Mountains was an abandoned mine that housed 150 hibernating bats in 1984, but the winter population declined to just a few individuals by 1986 as a likely result of disturbance (Saugey et al., 1988). The only known maternity colony in Alabama, reported to consist of about 8,000 bats in summer 1990, was reported as being "extremely vulnerable to destruction" because of disturbance and vandalism (Best et al., 1992:64). Another summer colony at a different cave was previously described as the largest in Alabama, but it had been extirpated by the mid-1980s. In Louisiana and eastern Texas, the southeastern myotis is considered widespread but rare (Lowery, 1974; Lance and Garrett, 1997; Mirowsky et al., 2004).

In Florida, where the species is considered most abundant (Amelon et al., 2006), populations occur in two regions: the panhandle and the north-central peninsula (Gore and Hovis, 1994). Humphrey and Gore (1992:335) caution that for Florida "uncertain accuracy of population estimates and ignorance of seasonal movements among caves precludes evaluation of trends from the scanty data available." Given this caveat, most of the existing information is suggestive of declines. Rice (1957) felt that in northern peninsular Florida he had located most of the maternity colonies in existence during the early 1950's (which may not have been the case [Gore and Hovis, 1994]), with most in just 6 caves. At that time Rice (1957) crudely calculated a total population of about 334,000 southeastern myotis at these caves. During the early 1990's, one cave that previously housed a colony of 2,500 (Rice, 1957) was gone, a second of 90,000 remained at about the same numbers, and a third of 30,000 was on a site scheduled for development of a housing project (Humphrey and Gore 1992). One report suggested that a summer population of 112,000 bats in the Florida panhandle had dropped to 31,000 by 1970 (Lee and Tuttle, 1970). Estimates of populations in four caves in the panhandle during 1987 to 1989 were: greater than 2,000, about 3,000, less than 50,000, and greater than 50,000. Three caves in the Florida panhandle that had previously supported populations, including a colony of 11,000 at one in the 1950s, were completely devoid of bats by the early 1990's (Humphrey and Gore, 1992), and another cave in the Florida panhandle with a maternity colony documented at 15,000 in 1970 had fewer than 200 in 1981 (Wenner, 1984).

Apparent declines at Florida caves prompted an intensive statewide survey for maternity colonies in 1991–92 (Gore and Hovis, 1994, 1998). Only nine caves in Florida harbored maternity populations, with 10 historic sites known to be used by southeastern bats at past times no longer occupied by bats. Caves with historical maximum population estimates (adults prior to parturition only) noted at various times from 1936–1982 totaled about 380,000 bats; in 1991–92 maxima of about 243,000 were estimated at these same sites and a total for all sites occupied in 1991–92 in both peninsular Florida and the panhandle combined was about 320,000 bats (Gore and Hovis, 1994, 1998). These numbers are suggestive of lower populations but are not directly comparable to earlier estimates because it is unknown how many of the earlier sites were continuously or simultaneously occupied, how many undiscovered populations had existed in the recent past, how much movement occurs among sites, and how methods of estimation may have differed. Most of the maternity colonies visited in 1991 or 1992 showed evidence of successful production of young, particularly in the panhandle, but just three of six caves in the peninsula occupied by females in spring 1992 had evidence of volant young by summer. The other three showed signs of disturbance (including fires beneath roosting sites) and abandonment.

Comer et al. (2014) compared detection probabilities for southeastern myotis using acoustic sampling versus roost search transects in eastern Texas pine habitat and found that 6 nights of acoustic surveys (using two detectors) would yield a detection probability of 90%, whereas 61 one-kilometer length transects would be required to attain the same detection probability using roost searches. In Mississippi, Fleming et al. (2013b) estimated that searches for roost trees of this species had detection probabilities above 90%, but that visual estimates of colony size by inspecting internal cavities underestimated numbers of bats compared to digital imagery, with increased error in larger colonies.

Management Practices and Concerns.— Although some maternity colonies of southeastern myotis can be found in buildings (for example, Hermanson and Wilkins, 1986), in Florida most young are born in caves (Gore and Hovis, 1994). These bats are thus very vulnerable where populations require caves for reproduction because of disturbance, blocking of entrances, destruction of cave habitat, and intentional killing. Populations are no doubt at greatest risk in Florida and other parts of the southeastern U.S. that are undergoing rapid conversion of habitat to support burgeoning populations of people. Humphrey and Gore (1992) reported that one colony of 11,000 known from the 1950's had become a public dump filled with trash and lacked bats completely, a colony of 2,500 at another site had been displaced because of frequent use of the cave for recreation, and that vandals throwing guano at roosting bats at a third site contracted histoplasmosis, resulting in demands to destroy the colony as a public health threat. Some former colony sites surveyed in Florida in 1991–92 had blocked entrances; several active maternity caves in Florida showed evidence of malicious disturbance, including fires, spent ammunition, and carcasses of killed females and neonates (Gore and Hovis, 1994, 1998). These observations are symptomatic of the large encroachments of people into formerly isolated areas of the southeastern U.S., and probably represent only a fraction of such incidents. Catastrophic mortality from natural sources such as flooding can also be an important issue for population dynamics when major segments of populations are aggregated at just a few locations (see "Mortality Factors" above).

Some caves in the Florida panhandle that have been protected for the endangered gray bat are also used by southeastern myotis, at least two other caves on public lands harboring primarily this species have been gated or fenced, and several caves on private lands have been posted against trespass to protect their colonies (Humphrey and Gore, 1992). Intentional removal of a gate by management at one of three entrances to Old Indian Cave at Florida Caverns State Park resulted in increased nightly egress of a mixed group of gray bats and southeastern bats (largely the latter), but with no overall change in abundance of the roosting population (Ludlow and Gore, 2000). The removed gate was replaced by a perimeter fence because managers felt it was advantageous to have multiple unobstructed entrances to reduce predation and increase efficiency of emergence, while still restricting access to the cave by potential trespassers (Ludlow and Gore, 2000).

Gore and Hovis (1994, 1998) recommend several measures for conservation of colony sites for this species in Florida, which may harbor a significant portion of the U.S. population. They stress the need for wider efforts at educating both veteran and novice cavers to avoid maternity colony sites at critical times of year (15 February to 15 August), to increase emphasis of enforcement of trespass laws, and to develop conservation easements, deed restrictions, special designations, or purchase of critical caves. The best approach to achieve these goals is development of a cooperative unified cave management plan aimed at conservation of all cave-roosting bat colonies in Florida (Gore and Hovis, 1994). Additional study of ecology and natural history, including foraging habitat requirements and possible impacts of contaminants was also recommended.

The only detailed information on southeastern myotis in relation to chemical contaminants is based on samples examined for cadmium, chromium, copper, lead, and zinc in northern Florida. Clark et al. (1986) reported that in comparison with a distant control colony, concentrations of cadmium were higher in guano, kidneys, and livers (but not at pathological levels) of bats exposed to metals that had been released into local streams from a battery salvage plant. Past attempts to eliminate colonies in buildings have used pesticides (Hermanson and Wilkins, 1986), but killing bats in roosts with chemicals is now illegal in many states.

In states other than Florida, the southeastern myotis may rely more heavily on hollow trees in bottomland hardwood forests than on caves or human-made structures. M.K. Clark (2003) reviewed information about their occurrence in these habitats and concluded that large historical losses and current rates of fragmentation of bottomland hardwood forests may have impacted their populations. Conservation of such habitats, including tracts with large hollow trees of species known to be used as roosts, will be of benefit to populations of this bat. Anecdotal observations in Texas have documented that roost trees used by southeastern myotis can be destroyed in severe storms and hurricanes (Stuemke et al., 2014). At Noxubee National Wildlife Refuge, the U.S. Fish and Wildlife Service has added openings to trees with cavities that had no previous access points for bats: southeastern myotis have been observed using these trees (Richardson, 2007). They also have been observed using cinder block towers built as experimental artificial roosts, as well as large "barn" or "community" bat houses such as those occupied by this species at the University of Florida in Gainesville (Bayless, 2006; Lacki and Bayless, 2013).

NOTES AND COMMENTS.— An estimated 90% of the potential habitat for this species occurs on private lands (Amelon et al., 2006). Bat Conservation International and the Southeastern Bat Diversity Network have developed a conservation and management plan for Rafinesque's big-eared bat and the southeastern myotis (Lacki and Bayless, 2013) that reviews additional detailed biological information, major threats and conservation needs, and provides well-considered specific suggestions for future research and conservation strategies. For more information see the account for Rafinesque's big-eared bat above.

Myotis ciliolabrum — Western small-footed myotis (Family Vespertilionidae)

CONSERVATION STATUS.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2010a, 2011b, 2015a): Sensitive Species (California, Idaho, Nevada state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G5, Secure.

State Designations: California Department of Fish and Wildlife (2017): Special Animals List. Kansas Department of Wildlife, Parks and Tourism (2005; Rohweder, 2015): Species of Greatest Conservation Need Tier II. Idaho Department of Fish and Game (2015): Species of Greatest Conservation Need Tier 3. Nevada Department of Wildlife (2013): Species of Conservation Priority. Nevada Department of Conservation and Natural Resources (2015a): Vulnerable, Watch List. North Dakota Game and Fish (Hagen et al., 2005; Dyke et al., 2015): Species of Conservation Priority Level III. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier II. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need. Washington Department of Fish and Wildlife (2015a): Species of Concern.

DESCRIPTION.— The western small-footed myotis (Fig. 23) is among the smaller bats of North America. "Typical" specimens often have dark face masks, long, dark ears, and dark wings that contrast with a pale, yellowish-brown pelage. The calcar is keeled. Examples of typical ranges of body masses and forearm lengths reported in the literature are 2.8 to 7.0 grams and 31.3 to 36.0

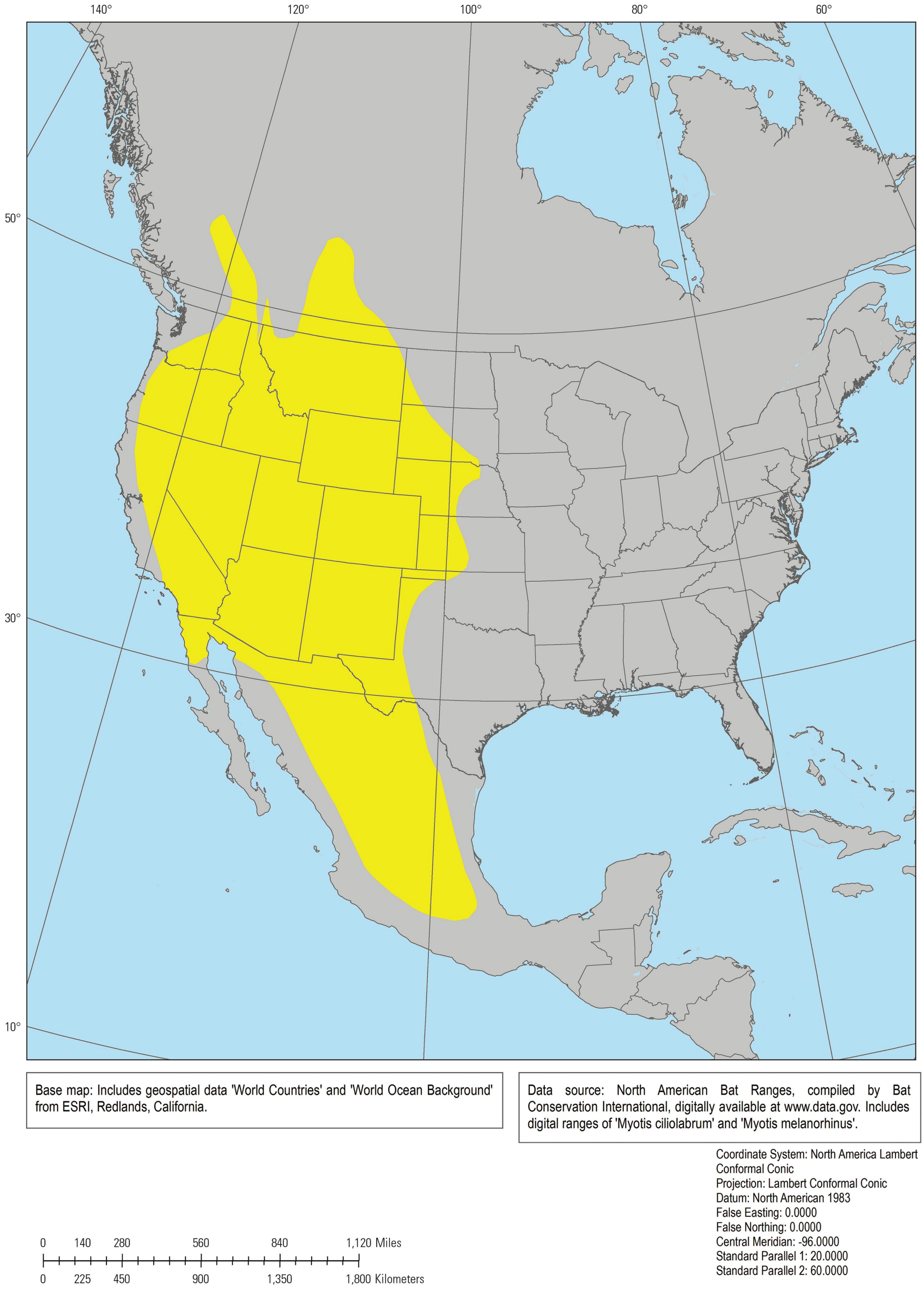
FIGURE 23. Western small-footed myotis, *Myotis ciliolabrum* (photo by J. Scott Altenbach).

millimeters (Bogan, 1974; Constantine, 1998b; Verts and Carraway, 1998; Rodriguez and Ammerman, 2004). Van Zyll de Jong (1985) reported that 50 individuals averaged 4.9 ± 1.1 (SE) grams in body mass and 32.2 ± 0.68 millimeters in forearm length. In a sample of hundreds of individuals from Alberta, Lausen (2007) reported geographic differences in forearm lengths and showed that females averaged slightly but significantly larger in forearm length than males, with measurements ranging from 29.0 to 38.9 millimeters across both sexes (692 individuals). In San Bernardino County, California, the tip of the tail is exserted about 1.5 to 2.5 millimeters beyond the tail membrane (Constantine, 1998b).

In some areas, *M. ciliolabrum* is sometimes difficult to distinguish from the closely related California myotis (*M. californicus*) even using external and cranial measurements, echolocation characteristics, or mitochondrial DNA (Bogan, 1974; Verts and Carraway, 1998; Higginbotham and Ammerman, 2002; Rodriguez and Ammerman, 2004; Zinck et al., 2004). Habitat also does not always adequately separate all individuals of these two species in such areas, whereas in other regions some external characters or cranial measurements appear sufficient to allow accurate identification (for example, Constantine, 1998b). For these reasons some field researchers report bats captured and released as combined *M. californicus*/*M. ciliolabrum* rather than attempting to distinguish among individuals (for example, Black, 1974; Hall, 2000; Chung-MacCoubrey, 2005; Geluso, 2008; Geluso and Geluso, 2012; O'Shea et al., 2016b).

DISTRIBUTION AND SYSTEMATICS.— The western small-footed myotis is found in western North America from Canada to central and southern Mexico (Fig. 24). In the United States, it is found from inland Washington, Oregon, and California (occurring on the Pacific coast only in southern California) eastward to western regions of the Great Plains states from Texas to North Dakota, also extending along the lower Missouri River in eastern South Dakota and Nebraska (Holloway and Barclay, 2001).

The literature on the distribution and systematics of this species can be confusing and includes apparent errors. These bats were considered to fall under the name *Myotis subulatus* up to the mid-1960s, but this name is no longer valid. Glass and Baker (1965) officially petitioned the International Commission on Zoological Nomenclature to formally suppress the name "*subulatus*", later noting (Glass and Baker, 1968) withdrawal of the proposal and instead formally designating a subspecies of the small-footed myotis (*Myotis leibii*) as *M. leibii ciliolabrum*. Van Zyll de Jong (1984) further refined understanding of the taxonomic status of these myotis by showing that there are two species of small-footed myotis in North America based on cranial morphology: *M. ciliolabrum* and *M. leibii*. This was later supported by electrophoretic protein analyses at 20 presumptive loci (Herd, 1987), and by molecular genetic analysis of nuclear amplified fragment length polymorphisms



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov. Includes digital ranges of 'Myotis ciliolabrum' and 'Myotis melanorhinus'.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 24. Approximate distribution of the western small-footed myotis, *Myotis ciliolabrum*.

(Ammerman et al., 2016). The eastern small-footed myotis retained the name *M. leibii* and the western small-footed myotis was justifiably designated with the name combination of *Myotis ciliolabrum*. Van Zyll de Jong (1984) also recognized two subspecies of the western small-footed myotis, *M. ciliolabrum ciliolabrum* and *M. ciliolabrum melanorhinus*, based on earlier usage (Merriam, 1886) of the subspecific names as specific epithets (then placed within the genus *Vespertilio*).

The nomenclature for *M. ciliolabrum* thus has been widely recognized for over 30 years (for example, Holloway and Barclay, 2001). A possible mistake in the interpretation of van Zyll de Jong's (1984) paper (which clearly listed the subspecies as *M. ciliolabrum ciliolabrum* and *M. ciliolabrum melanorhinus*) split *Myotis ciliolabrum* into two species-level names: *M. melanorhinus* west of the Rocky Mountains and *M. ciliolabrum* east of the Rocky Mountains (Simmons, 2005), but with no biological or nomenclatural justification for this division. For *Myotis ciliolabrum*, Simmons (2005) states "Formerly included in *leibii* (for which Hall [1981] used the name *subulatus*), but see van Zyll de Jong (1984). Does not include *melanorhinus*; see van Zyll de Jong (1984). Reviewed by Holloway and Barclay (2001), but note that they included *melanorhinus* as a subspecies of *ciliolabrum*." However, van Zyll de Jong (1984) gives *M. ciliolabrum melanorhinus* and *M. ciliolabrum ciliolabrum* as subspecific names and does not raise them to the species level, contrary to Simmons' (2005) interpretation. Bradley et al. (2014) do not include the name *M. melanorhinus* in their list of North American mammals. To our knowledge the nomenclature used by Holloway and Barclay (2001) is correct, and for this report we only consider the name *M. ciliolabrum* as valid for the species. Although there is no biological or nomenclatural basis in the published literature for the distinction and consequent elevation of the name *M. melanorhinus*, this new usage has appeared in a field guide (Kays and Wilson, 2009) and elsewhere. The field guide also gives the Continental Divide as demarcation of the two seemingly incorrectly designated species, but in many areas the Continental Divide extends down to habitats that are well used by this bat and does not constitute a continuous biological barrier. Holloway and Barclay (2001) provide a full taxonomic synonymy of past scientific names applied to the western small-footed myotis.

The generic name originates with Greek words meaning "mouse" and "ear". The specific epithet stems from Latin words meaning "eyelash" and "lip". Other common names include western small-footed bat, hairy-lipped bat, small-footed bat, black-nosed bat, Say's bat, and La Grulla brown bat.

Habitats and Relative Abundance.— In much of its range, the western small-footed myotis seems most abundant in forest and woodland habitat, although it is also found in lower-elevation habitats including the high plains in the Texas panhandle and rocky eroded terrain and badland cliffs in northeastern Colorado (Cary, 1911; Armstrong et al., 2011; Ammerman et al., 2012a). Potential exists for this species to be under-represented in capture samples from some regions due to difficulty distinguishing it from the California myotis. The California myotis is often presumed to be more abundant than the western small-footed bat in areas where they both occur, possibly resulting in reporting bias if western small-footed bats are not carefully identified and are erroneously assumed to be the more common species.

Pacific Northwest and Northern Rocky Mountains: *Oregon, Washington, and British Columbia*: Western small-footed myotis were of lower abundance in surveys over streams and ponds in Douglas fir-western hemlock forests across the western Cascade Mountains in southern Washington and the Oregon Coast Range, ranking seventh among 12 species (five bats among 241 individuals); they were more abundant among bats captured in the eastern Cascades, ranking first among 49 individuals of five species with 18 captured (Thomas, 1988). They ranked ninth in relative abundance (six bats sampled among 413 individuals of 11 species) of individuals collected for stomach contents analysis in arid scrubland and forest habitats of eastern Oregon (Whitaker et al., 1981). Captures of night-roosting bats at five bridges in western hemlock forest in the Willamette National Forest of Oregon included eight species and 412 individuals, but no western small-footed myotis (Perlmeter, 1996). This species ranked seventh in relative abundance (40 captures of 1,057 individuals of 11 species) of bats captured over water in the predominantly ponderosa pine forests of the eastern Cascade Mountains of south-central Washington (Baker and Lacki, 2004). This species ranked third in relative abundance (80 individuals) among 12 species and 958 bats captured over water in the semi-arid Okanagan Valley of southern British Columbia (Woodsworth, 1981). They ranked fifth in relative abundance (23 captures) in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water (Fenton et al., 1980).

***Montana*:** Western small-footed myotis were the most abundant of nine species (74 of 231 individuals) of bats captured over water in the Pryor Mountains of south-central Montana (Worthington, 1991).

California and Nevada: The first records of western small-footed myotis in California were at elevations from 1,340 to 1,830 meters in upper Sonoran to Transition zones (Grinnell and Swarth, 1913). They ranked seventh of 17 species (16 individuals among 390 bats) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999 (Pierson et al., 2001) but were not reported in a mist-net survey both over water and within forests (concentrating on groves of giant sequoia trees, *Sequoiadendron giganteum*) that recorded ten species and 284 individuals in Yosemite National Park (Pierson et al., 2006). Along montane areas around the upper Sacramento River in northern California, they were infrequently captured in mist nets set over water, numbering five bats among 1,398 captures of 15 species during four summers, ranking fifth least abundant (Pierson et al., 1996b). They were not observed using bridges as night roosts along the upper Sacramento River in montane hardwood and conifer habitats (elevations 320–730 meters), although 2,132 individuals of nine species of bats were documented using these structures at night (Pierson et al., 1996b). These bats also were not documented in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests, and 403 bats of 10 other species were captured (Duff and Morrell, 2007).

Western small-footed myotis were intermediate in abundance (33 captures), ranking sixth among about 2,000 bats of 13 species netted over water in the White and Inyo Mountain ranges of Nevada and California, where they were taken in upper Mojave and Great Basin desert scrub through piñon-juniper woodland habitats (Szewczak et al., 1998). In contrast, this was the most abundant species taken (80 individuals among 299 bats of 10 species) in mist nets over water across a variety of habitats ranging from 1,200 to over 2,800 meters in west-central Nevada (Kuenzi et al., 1999). They were the third most abundant bat found using a variety of mist-netting techniques and utilized all of six habitat categories in northeastern Nevada, ranging in elevation from 1,400 to 2,620 m (Ports and Bradley, 1996).

Southwestern U.S.: ***Arizona:*** Western small-footed myotis were relatively uncommon in capture records that were predominantly in desert habitats of western Arizona, where 66 individuals were taken among 3,458 bats netted over water (ranking tenth in relative abundance out of 17 species), with most appearing to have been taken in woodlands or forested habitats in mountains rather than in the more lowland desert; it was noted that these bats were not very susceptible to captures in mist nets (Cockrum et al., 1996). They ranked eighth in abundance among 17 species of bats (32 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). Western small-footed myotis ranked ninth in relative abundance (22 taken among 1,441 individuals) of 14 species captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). They ranked eleventh in relative abundance (three bats among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim, on the Tonto National Forest in central Arizona (Lutch, 1996). This species ranked eleventh in abundance among 15 species (17 bats captured among 1,673 individuals) netted over water in ponderosa pine and ponderosa pine-Gambel oak woodlands at 2,200 to 2,600 meters elevation on the Coconino Plateau of northern Arizona during 1993–1995 (Morrell et al., 1999).

New Mexico: Eighty-six western small-footed myotis (79% male) were captured over ponds, streams, and along cliff faces at 10 sites in the Jemez Mountains of New Mexico, ranging from 1,753 to 2,729 meters elevation and including piñon-juniper woodland, ponderosa pine, and mixed conifer forests; this was the sixth most frequently captured species among 15 species and 1,532 bats netted in the region during 1995–1997 (Bogan et al., 1998). Echolocation activity of these bats in the Jemez Mountains was commonly detected in riparian, conifer, piñon-juniper, and ponderosa pine habitat that had intensely burned 20 years earlier (Ellison et al., 2005). They ranked fourteenth in relative abundance (35 captures among 1,595 bats of 20 species) in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were most often captured in woodlands and evergreen forest above 1,524 meters (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, they ranked tenth of 19 species (14 captures among 1,004 individuals) and were taken at all three sites; habitat at capture sites ranged from riparian hardwoods at 1,465 meters to pine-spruce-fir forest at 2,620 meters elevation (Jones and Suttkus, 1972). One of these bats was captured in a survey documenting 6 species and 130 individuals netted over water in riparian habitat along the middle Rio Grande in the Bosque del Apache National Wildlife Refuge in central New Mexico, within a broader Chihuahuan Desert landscape (Chung-MacCoubrey, 1999).

Texas: This was the least abundant bat among 18 species captured across all habitats at Big Bend National Park in southwestern Texas, with a single bat taken (in woodland habitat) among 4,807 individuals (Easterla, 1973). None were captured in a subsequent study during 1996–1998 emphasizing lowland habitats at Big Bend National Park (among captures of 1,978 bats of 17 species; Higginbotham and Ammerman, 2002). They also ranked least abundant out of 14 species (one out of 542 individuals) captured in mist nets that sampled at 108 locations over water in northern Chihuahuan desert habitats at Big Bend Ranch State Park in the Trans-Pecos region of Texas; the single bat was captured over a small pool in a sparsely vegetated area within a canyon (Yancey, 1997). They were low in relative abundance (four captures out of 1,329 individuals in 12 species, ranking ninth) among bats captured in mist nets set over water at Palo Duro Canyon State Park in the Texas Panhandle, where habitats consisted of mesquite (*Prosopis glandulosa*) -juniper associations, grasses, cacti, and a riparian zone of cottonwood (*Populus deltoides*) and salt cedar (*Tamarix ramosissima*) set within sandstone, shale, and limestone canyon walls (Riedle and Matlack, 2013).

Central Rocky Mountains and Western Great Plains: *Colorado*: Western small-footed myotis ranked as the second most abundant species (72 captures among 546 bats of 11 species) captured over stock ponds during surveys in piñon-juniper woodland at about 2,100 meters elevation in the Uintah Basin of Moffat County in northwestern Colorado during 1979–1981 (Freeman, 1984). They ranked lower in abundance in other areas of Colorado. These bats were intermediate in abundance at Mesa Verde National Park in southwestern Colorado (fifth most frequently captured species, but with males outnumbering females) during mist netting of 1,996 bats of 15 species in piñon-juniper woodland, ponderosa pine, and mixed conifer forests during 2006–2007 (O'Shea et al., 2011a). In an earlier study at Mesa Verde National Park during 1989–1994, they also were intermediate in abundance, ranking fourth with 13 captures among 189 bats of 11 species (Chung-MacCoubrey and Bogan, 2003). This species was also intermediate in abundance (102 captured among 1,398 bats of 10 species, ranking sixth most frequently captured) among those taken in ponderosa pine and Douglas fir forests along the Colorado Front Range, primarily in Boulder County (Adams et al., 2003), and seventh of nine species (14 bats among 634 individuals) in similar habitats in adjacent Larimer County (O'Shea et al., 2011b). In contrast, they were apparently absent from Engelmann spruce-subalpine fir forests at 2,900 meters in the central Rocky Mountains of Colorado (Storz and Williams, 1996) and were rarely captured in urbanizing areas at Fort Collins, Colorado (ranking fifth of seven species, with two bats among 504 individuals; O'Shea et al., 2011b). In western Colorado, this species ranked seventh in abundance of 16 species (24 taken among 899 bats) captured at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Western small-footed myotis also ranked seventh in abundance (81 captures among 1,377 bats of 15 species) in mist-netting surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

***Utah*:** Western small-footed myotis ranked thirteenth in relative abundance of 15 species (eight individuals out of 572 bats) in the Henry Mountains of Utah, where they were netted over water at 2,335 to 2,713 meters elevation (Mollhagen and Bogan, 1997). None were captured at Arch Canyon on the Colorado Plateau in southeastern Utah where 295 bats of 15 species were taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016).

***Wyoming*:** Western small-footed myotis ranked third among 12 species (43 captured out of about 370 individuals) documented by mist netting in lower elevation basin and foothills habitat in the south-central part of Wyoming during 2012 (Abernethy et al., 2013). They were the least abundant (one of 112 individuals of seven species) captured in late summer-early autumn 2010–2011 by mist netting over water at elevations ranging from 1,568 to 3,116 meters in lodgepole pine, Engelmann spruce, subalpine fir, and Rocky Mountain juniper forests with open sagebrush and grassland habitats on the northern range of Yellowstone National Park, northwestern Wyoming (Johnson et al., 2017). They were not documented among 246 bats of six species captured in mist net surveys over streams and beaver ponds in and near the Medicine Bow National Forest in southern Wyoming, at elevations ranging from 2,133 to 2,896 meters and in habitats encompassing lodgepole pine (*Pinus contorta*) and spruce-fir forests (Gruver, 2002).

***South Dakota*:** Western small-footed myotis were the least abundant species captured during warm seasons in ponderosa pine-dominated habitat in the southern Black Hills of South Dakota, with 63 bats taken among 1,197 individuals of seven species (Cryan et al., 2000). However, they were the most common species in sampling at Badlands National Park in South Dakota (198 western small-footed myotis out of 405 bats of nine species; Bogan et al., 1996, see also Farney and Jones, 1980).

Alberta, Canada: Western small-footed myotis ranked as least abundant (two captures among 1,868 individuals) of eight species of bats mist-netted over water in riparian habitats through urban Calgary and surrounding prairies in Alberta, Canada (Coleman and Barclay, 2012). However, Lausen and Schowalter (2008) provided a composite tabulation of results of mist netting in areas with suitable roosting habitat across Alberta, allowing a crude estimate that about 30% of 3,137 bats captured in unpublished surveys were this species (but see notations on biases in Lausen and Schowalter, 2008).

Elevational Differences in Habitats among Sex and Age Classes: Male and non-reproductive female western small-footed myotis outnumbered reproductive females in ponderosa pine dominated habitats in western South Dakota, with reproductive females taken at lower mean elevations (Cryan et al., 2000); 171 of 198 (86%) captured at nine sites in Badlands National Park, South Dakota were males (Bogan et al., 1996). Lower-elevation records for females compared to males also have been reported during summer for northwestern Arizona (Cockrum et al., 1996), and a predominance of males at high-elevation forested areas was noted in New Mexico (Bogan et al., 1998), and at Mesa Verde National Park, Colorado, where most capture sites were at elevations greater than 1,890 m (O'Shea et al., 2011a).

FORAGING AND DIETARY ANALYSIS.— In north central Oregon, radio-tracked females emerged relatively early in relation to sunset and traveled down side canyons and along creeks to common foraging areas on the floodplain of the John Day River, from three to 12 kilometers distant from their separate roosts (Rodhouse and Hyde, 2014). Surrounding habitat was characterized as juniper woodland and sagebrush aridlands, above an area of both irrigated cropland and abandoned fields. Six of nine females radio tracked for two to eight nights used the same 2.5–kilometer-long oval shaped foraging areas over the floodplain each night, an area also used on some nights by the remaining three bats. Radio-tagged bats did not use night roosts, but some returned to day roosts for short (approximately 20–minute) periods, presumably to nurse young, whereas later in the summer females remained away from roosts foraging for about four hours (Rodhouse and Hyde, 2014). Females foraged in small circuits about two to five meters high over the floodplain (including irrigated crop fields), slopes, rock outcrops, and the river. In the Huachuca Mountains of southeastern Arizona, they were observed foraging in the oak woodland vegetation belt of the Upper Sonoran desert life zone (Hoffmeister and Goodpaster, 1954).

In northeastern Oregon, western small-footed myotis are reported to feed primarily on lepidopterans, hemipterans, and dipterans (Whitaker et al., 1981). Lepidopterans and coleopterans were the most often encountered groups seen in dietary analysis of fecal samples from northern Arizona ponderosa pine forest, with dipterans, neuropterans, hymenopterans, and hemipterans also consumed (Warner, 1985). Dietary analysis of stomach contents of western small-footed myotis from northwestern Colorado indicated that coleopterans were the major dietary component, followed by lepidopterans and trichopterans in descending order of proportional frequency, with other groups of insects each constituting less than 10% (Armstrong et al., 1994). Stomach contents of two individuals from southeastern Montana contained finely masticated remains of small beetles, lepidopterans, homopterans (cicadellids), dipterans, and trichopterans (Jones et al., 1973). In the semi-arid Okanagan Valley of southern British Columbia, analysis of feces from bats captured mainly over water revealed predominantly trichopterans, followed by dipterans, lepidopterans and coleopterans in descending order of proportional frequency (Woodsworth, 1981). In this region, the diet was comparable to the similarly sized, sympatric California myotis, but the two species tended to forage in different habitats: western small-footed myotis favored areas over rocky bluffs and California myotis fed over river banks (Woodsworth, 1981). These observations are similar to earlier notes from the same region that indicated that this species foraged over edges of rock cliffs and from one meter above ground to tree height when in wooded areas (Fenton et al., 1980).

Western small-footed myotis were among the species group sampled by Adams et al. (2003) that preferred drinking at watering places with higher concentrations of calcium and other minerals, perhaps providing a supplement to dietary intake that would be most critical to reproductive females and weaned volant juveniles.

ROOSTING HABITS.— Winter Roosts: Jagnow (1998) found these bats in hibernation in low numbers (seven to 111 bats, varying by year) in small groups ranging in size from solitary individuals to clusters of up to 25 bats at Torgac Cave, New Mexico. This species also has been reported hibernating in small numbers singly at Crocodile Cave in Kane County, Utah and at Logan Cave in northeastern Utah (Hardy, 1941; Twente, 1960). Western small-footed myotis were mostly seen hibernating in small numbers in abandoned mine tunnels in Nevada, where they roosted on ceiling surfaces and not within deep crevices (Alcorn, 1944). They were one of the more commonly found species hibernating in abandoned mines in Great Basin desert scrub and piñon-juniper woodlands of the White and Inyo Mountains in California and southwestern Nevada, where they were seen hibernating as single individuals, often within crevices, and not in clusters (Szewczak et al., 1998). Similar findings were reported for abandoned mines used as hibernacula in west-central Nevada, where these bats were found hibernating at air temperatures averaging 5.2ºC (range 1.0 to 17ºC) and at a mean relative humidity of 48% (range 24 to 66%; Kuenzi et al., 1999). Also in Great Basin desert scrub, hibernating individuals used six of 31 lava tubes examined in Idaho, where they wedged themselves into crevices in the ceilings and were observed in hibernation in various caves at air temperatures ranging from 0.9 to 4.7ºC (mean 2.4ºC) and levels of relative humidity ranging from 62 to 85% (Genter, 1986). In Washington and Oregon, these bats were the second most frequently encountered bat found hibernating in searches of 650 caves or mines during winters 1982–1989, with 35 found at nine caves and one mine, with one to six bats per site roosting singly (Perkins et al., 1990). One was found apparently hibernating in a stone cornice of a building in Oregon during November (Perkins et al., 1990).

Western small-footed myotis have been observed hibernating in a mine at 2,895 meters in southwestern Colorado (Armstrong et al., 1994). Small numbers also hibernate in irrigation tunnels in northeastern Colorado (Armstrong et al., 1994) and in an abandoned copper mine in southeastern Colorado (Ellinwood, 1978). A survey during 1969–1970 reported them hibernating in numbers ranging from one to at least 20 in seven caves and mines ranging from 1,158 to 1,615 meters elevation in the Black Hills of South Dakota; bats wedged themselves into tiny crevices and were mostly solitary, but with up to four within a crevice (Martin and Hawks, 1972). In winter, counts of this species during hibernation at Jewel Cave were 20 or fewer, amounting to less than 1% of all hibernating bats of at least seven species seen in the cave over the course of multiple winters 1967–1993 (Choate and Anderson, 1997).

Western small-footed myotis were seldom encountered flying in winter at low-elevation arid areas in southern and central New Mexico, representing just 1% (four individuals) of 401 bats of 12 species documented in winter activity surveys (in contrast, 59 California myotis were captured from November to March); three of the four western small-footed myotis were taken in March and had been feeding (Geluso, 2007). Winter activity of this species was also detected acoustically during warmer periods on prairies in southern Alberta, Canada (Lausen and Barclay, 2006).

Although most searches for hibernating western small-footed myotis have concentrated on caves and mines, relatively small numbers have been detected in such roosts. We suspect that in many areas these bats hibernate in inconspicuous rock crevices, similar to big brown bats (*Eptesicus fuscus*) in Colorado (Neubaum et al., 2006) and Alberta, Canada (Klüg-Baerwald et al., 2017), and as postulated by Twente (1960) for western bats in general. These bats roost in rock crevices during summer (see below), winter flight activity has been documented near known summer crevice roosts (Lausen and Barclay, 2006), and the closely related eastern small-footed myotis has been found to roost in rock crevices during summer and months immediately prior to or after winter (see below). A single individual was captured and radio tagged at Yellowstone National Park in early autumn 2011 and only used rock crevices near the ground until the transmitter likely failed in mid-October (Johnson et al., 2017).

Warm Season Roosts in Rock and Soil Crevices and Cavities: Summer roosting habits of western small-footed myotis have not been widely studied, but identified roosts include rock crevices and erosion cavities. Tuttle and Heaney (1974) searched by eye and hand for roosts in the Badlands of South Dakota during July 1972 and found 12 active roosts occupied by 27 individuals. Roosts were located in horizontal fissures in large flat boulders or in small crevices or cavities (openings averaging 2.3 by 3.7 centimeters, depths averaging 16.7 centimeters) in sedimentary rock on eroded hillsides or vertical banks. Most roosts faced westerly or southerly directions. Ten roosts had either a single bat, or a bat with an offspring, one roost held four lactating females and five non-volant juveniles, and another roost had two adult females and one offspring; one adult male was found roosting solitarily about 0.4 kilometers from the area where females were found (Tuttle and Heaney, 1974).

Roosts of western small-footed myotis were discovered through radio tracking bats captured in the South Saskatchewan River valley, near Bindloss, Alberta, a badlands area with short-grass prairie dissected by coulees and exposed sandstone and mudstone cliffs and hoodoos (Lausen, 2007). Eighteen females (15 lactating or pregnant) were tracked to 30 roosts. Roosts were found either in mudstone or harder, boulder-like substrates. More roosts were in small cavities (erosion holes) or crevices in mudstone than were in solid boulders, and roosts were usually occupied by only one or two bats (mean group size of 1.4 ± 0.2, range one to five; Lausen, 2007). Roost switching was frequent, with individuals rarely using the same roost on consecutive days but moving a mean distance of 45 meters between roosts (range 6.4 to 106 meters). The first roost discovered for each of the tracked bats ranged from four to 580 meters from the point of capture (mean 146 ± 23 meters). Openings to roosts used by pregnant females were 20.2 ± 6.5 square centimeters and did not differ from openings to roosts used by lactating bats (38.4 ± 19.6 square centimeters), but both were significantly smaller than those of randomly selected crevices (301 ± 58 square centimeters); roost entrances faced south more often than randomly available crevices but were not different in distance from flat ground above and below, depth, slope, and crevice orientation (Lausen, 2007). Roosts chosen during lactation warmed more quickly after sunrise than roosts used during pregnancy.

In central Oregon, nine female western small-footed myotis were radio tracked during summer at John Day Fossil Beds National Monument (Rodhouse and Hyde, 2014). They roosted in small crevices (oriented both vertically and horizontally) in rock outcrops in small canyons and to a lesser degree in larger cliffs; roosts averaged 4.5 meters above ground but roosts of lactating females were situated higher than those of post-lactating females (Rodhouse and Hyde, 2014). Roosts were located 0.3 to 10.5 kilometers from the over-water capture sites. They primarily roosted solitarily, but group sizes of two to 15 bats were observed; lactating females roosted in groups but post-lactating females roosted alone. During the nine- to 12-day tracking periods roost switching occurred almost daily with a total of 43 roost locations discovered; just eight roosts were used twice on consecutive days, one roost was used for four consecutive days, and all others were used just once (Rodhouse and Hyde, 2014). Most females showed fidelity to a broad roosting area, with roosts ranging 30 to 347 meters apart within these areas. Similar to findings in Oregon, Cryan (1997) found two females roosting together during summer in a narrow (two centimeters) crevice 10 centimeters deep in a broken rock at the base of a sandstone cliff. Quay (1948) reported a male and a female roosting solitarily in small pockets under different sheets of rock in western Nebraska, and Neubaum (2017) radio tracked a lactating female to a crevice in a boulder in western Colorado.

Warm Season Roosts in Buildings, Under Tree Bark, and in Swallow Nests: A maternity colony numbering over 37 adult and young western small-footed myotis was reported roosting between the interior wall and loose wallpaper in an abandoned house in San Luis Obispo County, California (Koford and Koford, 1948). A maternity colony also was observed roosting in the attic space of a residence near Fort Collins, Colorado (O’Shea et al., 2011b). In Nebraska, a few have been taken from barns (Webb and Jones, 1952), a solitary bat was found roosting between two boards leaning on a shed (Stephens, 1945), and two bats were reported roosting under a loose strip of bark (Swenk, 1908). They have been found roosting in swallow nests in western Kansas (Merriam, 1886).

Warm Season Roosts in Caves, Mines, and Night Roosting: Bat captures made at the entrance to Jewel Cave in South Dakota using a harp trap were dominated by western small-footed myotis, with this species accounting for 222 of 587 bats of seven species, nearly all males (Choate and Anderson, 1997). In contrast, this species accounted for just nine captures out of 209 bats of nine species netted in summer over watering places near Jewel Cave (Choate and Anderson, 1997). It was unclear if the bats taken at the entrance to Jewel Cave were exiting the cave at emergence or entering the cave as a night roost. These bats were observed at eight caves in Colorado, averaging two bats per cave, although it also was unclear if observations were of night-roosting bats or bats roosting internally during the day (Siemers, 2002). Similarly, small numbers of individuals were captured in mist nets at the mouth of Azure Cave at 1,361 meters elevation in Montana during June to October (Hendricks et al., 2000). In Colorado, they were among the top four species found using abandoned mines, based on a sample of 1,903 bats of 11 species found in nine years of surveys at 1,800 sites (counts or other details not specified; Navo et al., 2000).

Western small-footed myotis use night roosts after feeding, as has been documented at several mines and caves in the Black Hills of South Dakota (Turner, 1974). They were not observed using bridges as night roosts along the upper Sacramento River in northern California (elevations 320–730 meters), although several other species of bats were well documented using these structures during the night (Pierson et al., 1996b). In contrast, bridges were used as night roosts of this species in the central Sierra Nevada of California (elevations greater than 1,000 m; Pierson et al., 2001).

Population Ecology.— **Litter Size, Natality, and Female Reproduction:** Cockrum (1955) summarized records for nine female western small-footed myotis from multiple locations, each with single embryos. Subsequently at least three females with single young were also reported from South Dakota (Turner and Jones, 1968; Turner, 1974; Farney and Jones, 1980), three females with one embryo each were taken in southwestern North Dakota (Genoways and Jones, 1972), as were two females in Nebraska (J.K. Jones, 1964; Geluso and Geluso, 2016), a single female from southeastern Montana (Jones et al., 1973), and a female from northwestern Colorado (Finley et al., 1983). However, one case of twinning in addition to three cases of singletons were reported in a roost in the Badlands of South Dakota (Tuttle and Heaney, 1974).

Natality estimates for western small-footed myotis can vary greatly but are sometimes low compared to estimates for other species. In prairie badlands of southern Alberta, an overall reproductive rate of 351 adult females captured away from roosts during the lactation period in summers 2001–2005 was 56% (Lausen, 2007). In southeastern Montana, one of six females taken over water was reproductive (Jones et al., 1973). Eleven of 14 females taken at Badlands National Park on June 30 and July 3, 1970 were reproductive (Farney and Jones, 1980). The proportions of adult females captured at watering places in southwestern Colorado that were reproductive varied with the amount of spring precipitation, averaging 30% in 20 females during a drought year and 63% in 27 females the following year, when spring precipitation and corresponding warm-season insect abundance were higher (Snider, 2009; O'Shea et al., 2011a). Twenty-one of 51 adult females (41%) captured during summer in west-central Nevada were reproductive (Kuenzi et al., 1999). Fourteen of 18 (78%) females captured over water in the Jemez Mountains of New Mexico during 1995 to 1997 (including a drought year) were reproductive (Bogan et al., 1998). Each of seven females (100%) netted over water or taken by shooting in the Mogollon Mountains in New Mexico and Arizona was reproductive during June and July 1960 to 1961 (C. Jones, 1964).

Cryan (1997) reported 83% of 12 female western small-footed myotis captured over water in the Black Hills of South Dakota as reproductive. Two of six females (33%) netted in southwestern North Dakota were reproductive (Genoways and Jones, 1972). In the panhandle of Nebraska, seven of 11 adult females (64%) were reproductive during 2010–2011 (Geluso and Geluso, 2016). Remarkably, the proportion of reproductive females among the cumulative total females taken over water over all U.S. locations and years was identical to the Alberta study, at 56% (96 of 172 bats). Natality at a maternity roost in San Luis Obispo County, California, was approximately 84% (16 non-volant young and 19 adult females captured, two unknown sex adults escaped; Koford and Koford, 1948). Tuttle and Heaney (1974) found nine of 10 females (90%) roosting primarily solitarily to be reproductive at Badlands National Park in South Dakota.

We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction, such as age at first reproduction and inter-birth intervals.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Mortality factors impacting western small-footed myotis are poorly known. Rabies infections have been documented (for example, Bogan and Cryan, 2000). Deaths due to entrapment in oil sludge pits in northwestern Colorado have been reported (Finley et al., 1983). White-nose syndrome has not been reported for this species. Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with anti-fungal properties on wings of these bats and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America. Helminths and ectoparasites have been described (as summarized by Sparks and Choate, 2000 and Whitaker and Wilson, 1974; see also Lausen, 2005; Heddergott and Steinbach, 2015) but no associated mortality has been observed.

Population Trend: Annual counts of western small-footed myotis at two hibernacula in New Mexico and South Dakota were analyzed for trends over time, but none were detected (Ellison et al., 2003). Species dynamic distribution models were constructed using Bayesian hierarchical modeling techniques for 12 species of bats in Washington and Oregon based on an eight-year monitoring program; bat activity was sampled with mist nets and acoustic detectors, and the analysis accounted for detectability and annual turnover in bat occurrence (Rodhouse et al., 2015). Western small-footed myotis did not show a decline in occurrence probabilities with time (Rodhouse et al., 2015).

Population Genetics: Lausen (2007) analyzed mitochondrial and nuclear DNA of 486 western small-footed myotis from prairies of Alberta to investigate genetic aspects of population structure, relatedness, and dispersal. Populations in that study region were highly structured and showed limited dispersal. Although the study did not directly address genetic diversity concerns, no present-day loss-of-diversity issues seemed apparent in the reported findings.

MANAGEMENT PRACTICES AND CONCERNS.— Protection of colony sites of this bat at abandoned mines through utilization of bat-compatible closure methods has been undertaken by the National Park Service at Guadalupe Mountains National Park (Burghardt, 2000). Numbers of these bats in hibernacula have not responded negatively to seasonal closures and bat-friendly gates at Torgac Cave on Bureau of Land Management property in New Mexico (Jagnow, 1998), and at Jewel Cave National Monument in South Dakota (Choate and Anderson, 1997). In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that California/western small-footed myotis (*M. californicus* and *M. ciliolabrum* not differentiated) continued using gated mines over the long-term, tolerated various gate designs, and that the landscape location and structural complexity of a mine were better predictors than gate characteristics of whether this species would continue using a site after gating.

Myotis evotis — Long-eared myotis (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. Bureau of Land Management (2009b, 2010a,b, 2011b, 2015a): Sensitive Species (California, Idaho, Montana, Nevada, North Dakota, South Dakota, Wyoming state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G5, Secure.

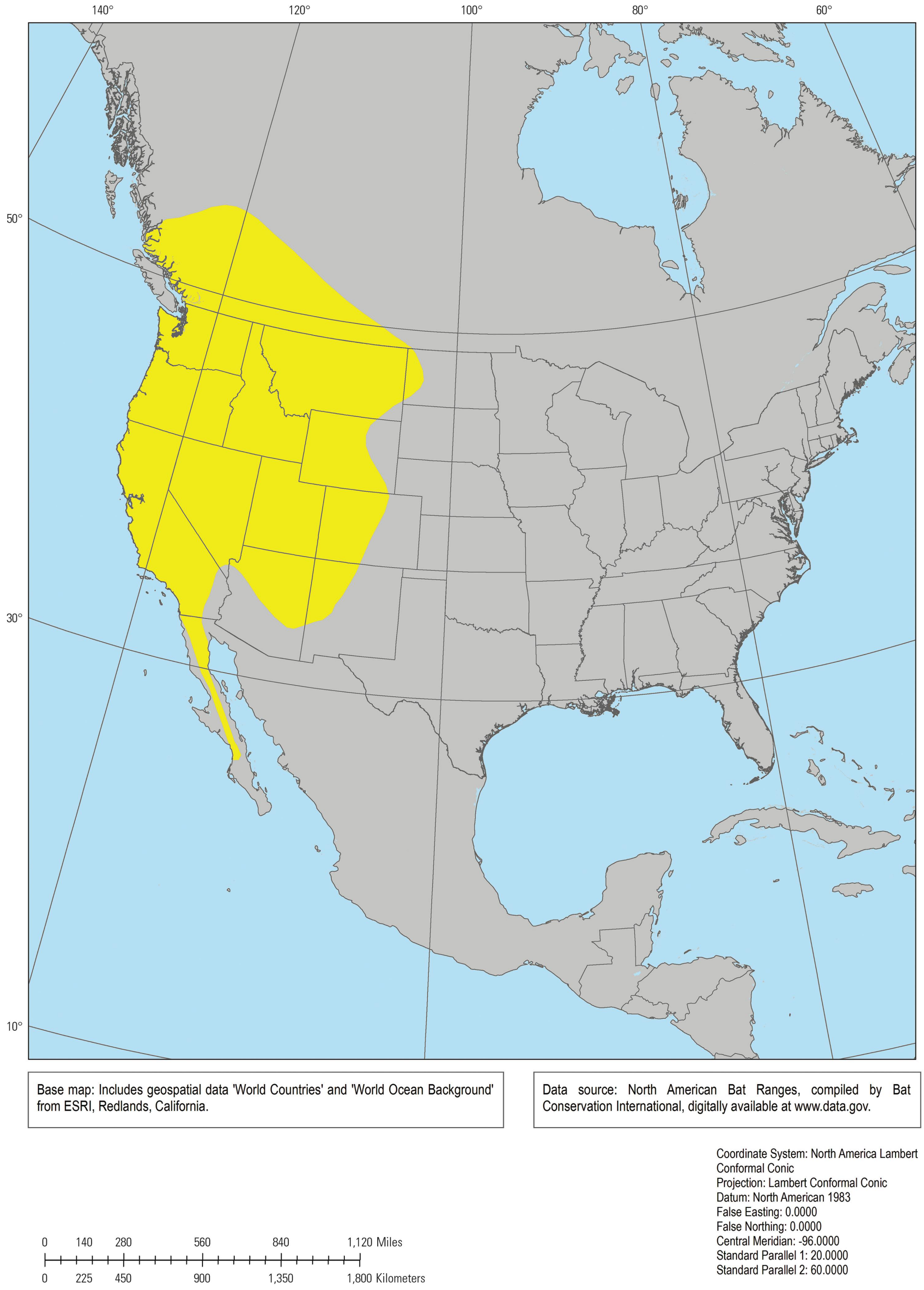
State Designations: Arizona Game and Fish Department (2012): Tier 1C Species of Greatest Conservation Need. California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. North Dakota Game and Fish (Hagen et al., 2005; Dyke et al., 2015): Species of Conservation Priority Level III. Nevada Department of Wildlife (2013): Species of Conservation Priority. Washington Department of Fish and Wildlife (2015a): Species of Concern. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier III.

Figure 25. Long-eared myotis, *Myotis evotis* (photo by J. Scott Altenbach).

Description.— This is a medium to large myotis with notably long ears (Fig. 25). The long-eared myotis has brown to straw-colored, soft, long (about 10 millimeters mid-dorsally) glossy dorsal pelage with blackish bases to hairs; the pelage contrasts markedly with the wing membranes and the dark, blackish ears that extend five millimeters or more beyond the tip of the snout when laid forward (Manning and Jones, 1989). Forearm lengths range from approximately 35–41 millimeters, ears are greater than 15–16 millimeters long, and body mass typically ranges five to eight grams (Manning and Jones, 1989; Verts and Carraway, 1998; Solick and Barclay, 2006a; Armstrong et al., 2011). A minute fringe of short hairs can sometimes be discerned on the trailing edge of the tail membrane, but these are much less conspicuous than in the fringed myotis (*M. thysanodes*). Some individuals in western Washington can overlap in cranial and external morphology with Keen's myotis, *Myotis keenii* (Van Zyll De Jong and Nagorsen, 1994).

Distribution and Systematics.— The long-eared myotis occurs in western North America from Baja California, Mexico to southern British Columbia, Alberta, and Saskatchewan, Canada (Fig. 26). In the United States, it is found in suitable habitat in western North and South Dakota, Wyoming, Colorado, New Mexico, Arizona, Utah, Montana, Idaho, Nevada, California, Oregon, and Washington.

Six subspecies are recognized (Manning, 1993), with four known from the United States: *Myotis evotis evotis*, found in the coastal range of California from the San Francisco area southward; *Myotis evotis chrysonotus*, found in southeastern Oregon, northern and central California



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 26. Approximate distribution of the long-eared myotis, *Myotis evotis*. Species range is shown in yellow, but extends farther east to western South Dakota (see text).

(Sierra Nevada), Idaho, Nevada, Utah, central and eastern Montana, western North and South Dakota, Wyoming, Colorado, and northern New Mexico; *M. evotis pacificus,* found in Washington, western and northern Oregon, coastal northwestern California, northern Idaho, and northwestern Montana; and *M. evotis jonesorum,* found in northern Arizona, and the Mogollon Rim of Arizona and New Mexico (Manning, 1993). Two other subspecies occur in Baja California. More definitive determination of the true taxonomic status of these two subspecies (*M. evotis micronyx* and *M. evotis milleri*) will require more intensive study (the latter subspecies is sometimes considered to be a full species, *Myotis milleri*; see Alvarez-Castañeda and Bogan, 1997). Taxonomic synonymies of past scientific names applied to this species are detailed by Manning (1993) and Manning and Jones (1989). Discussion of possible groupings within *M. evotis* and among *M. evotis* and other *Myotis* species based on molecular genetic relationships are provided by Zinck et al. (2004), Dewey (2006), Stadlemann et al. (2007), Carstens and Dewey (2010), and Vonhof et al. (2015). These studies suggest close evolutionary relationships of the long-eared myotis, fringed myotis (*M. thysanodes*), Keen's myotis (*M. keenii*), and one subspecies of the little brown myotis (*M. lucifugus carissima*). Evolutionary relationships among some of these species based on morphology and other traits also have been hypothesized (for example, Reduker et al., 1983).

The generic name originates with Greek words meaning "mouse" and "ear". The specific epithet stems from the Greek words for "good" and "ear". Other English common names found in the literature include western long-eared myotis, western long-eared bat, long-eared bat, little long-eared bat, golden-backed bat, desert golden bat, and little big-eared bat.

HABITATS AND RELATIVE ABUNDANCE.— Relative abundance of long-eared myotis varies with region and habitat. This species appears to be rare in urban and urbanizing environments of northern Colorado and near Calgary, Alberta compared to surrounding, less developed areas (O'Shea et al., 2011b; Coleman and Barclay, 2012).

Pacific Northwest and Northern Rocky Mountains: *Oregon, Washington, and British Columbia*: Long-eared myotis have been described as the most abundant bat across a variety of forest types in northeastern Oregon, and ranked as most abundant (121 bats sampled among 413 individuals of 11 species) collected for stomach contents analysis in arid scrubland and forest habitats (Whitaker et al., 1981). Similarly, they were the most abundant of 11 species (389 of 1,057 individuals) of bats captured over water in the predominantly ponderosa pine forests of the eastern Cascade Mountains of south-central Washington (Baker and Lacki, 2004). These bats were of lower abundance in surveys over streams and ponds in Douglas fir-western hemlock forests across the Cascade Mountains in southern Washington and the Oregon Coast Range, ranking sixth among 12 species (seven bats among 241 individuals) in the western Cascades, and were least abundant among five species captured in the eastern Cascades (one captured among 49 individuals; Thomas, 1988). Captures of night roosting bats at five bridges in western hemlock forest in the Willamette National Forest of Oregon included eight species and 412 individuals, but only four long-eared myotis (ranking fifth in relative abundance; Perlmeter, 1996). They ranked seventh in relative abundance (eight individuals) among 12 species and 958 bats captured over water in the semi-arid Okanagan Valley of southern British Columbia, where habitats included open areas and ponderosa pine forests (Woodsworth, 1981). They also ranked seventh in relative abundance (13 captures) in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water (Fenton et al., 1980).

***Montana and Alberta, Canada*:** These bats ranked sixth in relative abundance of nine species (13 of 231 individuals) of bats captured over water in the Pryor Mountains of south-central Montana (Worthington, 1991). Long-eared myotis were the most commonly captured bat in lodgepole pine forests of the Rocky Mountains of Alberta, with 221 bats captured among 417 individuals (Barclay, 1991).

California and Nevada: Vaughan (1954) observed long-eared myotis at elevations ranging from 850 to 2,500 meters in the San Gabriel Mountains of southern California (down to 1,800 meters on the inland desert slope) in habitats ranging from chaparral to ponderosa pine; at lower elevations they were seen foraging over water and among alders (*Alnus* sp.) and seep willow (*Baccharis* sp.), whereas at higher elevations they were observed foraging about two meters above ground among trunks of conifers. Woodland habitats seemed most preferred (Vaughan, 1954).

Relative abundance of individuals was low in mist net and night roost surveys along the upper Sacramento River of California, with 20 bats captured among 1,398 captures of 15 species in montane hardwood and conifer habitats (Pierson et al., 1996b). Long-eared myotis also were low in relative abundance (13 bats captured among 403 bats of 10 species) in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests (Duff and Morrell, 2007). This species ranked seventh among ten species in relative abundance (13 captures out of 284 individuals) in a mist-net survey both over water and within forests (concentrating on groves of giant sequoia trees, *Sequoiadendron giganteum*) in Yosemite National Park in the California Sierra Nevada Range (Pierson et al., 2006). This species ranked eighth of 17 (12 individuals among 390 bats) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999 (Pierson et al., 2001).

Long-eared myotis ranked eleventh in relative abundance (12 of about 2,000 bats) among 13 species captured foraging in four vegetation zones (ranging from desert scrub to bristlecone-limber pine forests) in the White and Inyo Mountains of Nevada and California, but they were only taken in lower drainages from Great Basin desert scrub through piñon-juniper habitats (Szewczak et al., 1998). They ranked eighth in relative abundance at the Nevada Test Site (56 among over 2,000 bats of 13 species), where all individuals were netted in Great Basin Desert habitat (Hall, 2000). This species ranked fifth (19 captures among 299 bats of 11 species) in mist-netting surveys over water in west-central Nevada in habitats categorized in four vegetation zones, but it was only taken in two, the piñon-juniper woodland and riparian deciduous zones (Kuenzi et al., 1999).

Southwestern U.S.: This species is unknown from the lower arid regions of the southwest, including Texas and parts of Arizona and New Mexico, areas considered outside of the species distributional limits (Manning and Jones, 1989). This has been confirmed by some extensive surveys. None have been captured in major surveys in and near Big Bend National Park in southwestern Texas (Easterla, 1973; Yancey, 1997; Higginbotham and Ammerman, 2002), in predominantly arid habitats of northwestern Arizona (but including pine forest and elevations at 2,286 m; Cockrum et al., 1996), and in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim, on the Tonto National Forest in central Arizona (Lutch, 1996).

***Arizona*:** Long-eared myotis ranked third in abundance among 15 species (269 bats captured among 1,673 individuals) netted over water in ponderosa pine and ponderosa pine-Gambel oak woodlands at 2,200 to 2,600 meters elevation on the Coconino Plateau of northern Arizona during 1993–1995 (Morrell et al., 1999). Long-eared myotis ranked third in relative abundance (243 captures among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). They ranked as least abundant among 17 species of bats (one captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). Absence of long-eared myotis in some surveys in Arizona (Cockrum et al., 1996; Lutch, 1996) is noted above.

***New Mexico*:** Long-eared myotis were commonly associated with piñon-juniper woodlands in the Cibola National Forest of New Mexico, where they were the third most abundant species taken in mist nets (176 captured among 1,222 bats of 10–11 species) and were found at most capture sites in the Gallinas Mountains (Chung-MacCoubrey, 2005). In the Jemez Mountains of New Mexico, they ranked fourth in abundance with 106 taken among 1,532 individuals of 15 species captured, with males occupying higher elevations and females mostly encountered in lower-elevation habitats (Bogan et al., 1998). Echolocation activity of these bats was commonly detected in riparian, conifer, piñon-juniper, and ponderosa pine habitat that was intensely burned approximately 20 years prior in the Jemez Mountains (Ellison et al., 2005). They also ranked third in relative abundance (25 among 302 bats of 10–11 species) among bats netted over water in mostly ponderosa pine habitat at 2,600 to 2,885 meters on Mount Taylor in northern New Mexico (Geluso, 2008). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species with 87 individual long-eared myotis, ranking eighth in relative abundance (Geluso, 2006, 2017).

Three studies assessed the relative abundance of bats at various locations in the San Mateo Mountains of west-central New Mexico. In ponderosa pine habitat of the Cibola National Forest, these bats were the second most abundant species taken (94 captured among 447 bats of seven to eight species) and also were found at most capture sites (Chung-MacCoubrey, 2005). Geluso and Geluso (2012) reported that they were the most abundant bat (536 captures among 1,390 bats and 11 species) taken over a 34-year period at a pond in coniferous forest at 2,573 meters elevation in the San Mateo Mountains of New Mexico. They were low to intermediate in abundance, ranking eighth among 16–17 species (15 captures out of 855 individuals) in mist-net captures over ponds during 1970 at Nogal Canyon, Socorro County, in habitats described as pinyon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974). This species ranked tenth in relative abundance (61 captures among 1,595 bats of 20 species) in the Mogollon Mountains of western New Mexico and adjacent Arizona, including a site in the San Mateo Mountains, and it was most often captured in evergreen forest (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, long-eared myotis ranked sixth of 19 species (77 captures among 1,004 individuals) and were taken at the two high sites in pine-spruce-fir forests at 2,438 and 2,620 meters elevation (Jones and Suttkus, 1972). Somewhat farther south, Jones (2016) documented bats captured during surveys of various habitats in the Greater Gila region of Catron, Grant, and Sierra Counties of New Mexico; they ranked as least abundant, with one capture among 282 individuals of 16–17 species (Jones, 2016; including data from unpublished reports of others).

Central Rocky Mountains: *Colorado*: The long-eared myotis was the second-most abundant species (186 bats) among 15 species and 1,996 individuals captured in mist nets in largely piñon-juniper and ponderosa pine habitats of Mesa Verde National Park, Colorado in 2006 and 2007 (O’Shea et al., 2011a) and the most abundant species taken there during 1989–1994, with 73 bats captured among 189 individuals of 11 species (Chung-MacCoubrey and Bogan, 2003). Differences in relative abundance between the two studies were probably due to greater selection of smaller pools of water for netting during the earlier work: small pools were less available during the 2006–2007 study but were likely more easily approached for drinking by the highly maneuverable long-eared myotis than by other species (O’Shea et al., 2011a). These bats were the most abundant species (257 captures among 546 bats of 11 species) captured over stock ponds during surveys in piñon-juniper woodland at about 2,100 meters in the Uintah Basin of Moffat County in northwestern Colorado during 1979–1981 (Freeman, 1984). They were reported from Engelmann spruce-subalpine fir forest in the subalpine zone in west-central Colorado at an elevation of 3,100 meters (an elevational record) but were uncommon, with only two bats netted among 111 bats of four species (Storz and Williams, 1996). In western Colorado, this species ranked fourteenth in relative abundance of 16 species (two among 899 bats) captured at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017).

In Boulder County, Colorado, long-eared myotis were moderately abundant in ponderosa pine and Douglas fir/mixed conifer forests, ranking third in abundance among 10 species and 1,398 individuals taken at the Boulder County sites (Adams et al., 2003). They ranked sixth of nine species (38 bats among 634 individuals) in similar habitats in adjacent Larimer County, Colorado but were most abundant above 2,000 meters (O'Shea et al., 2011b). This species ranked third in abundance (162 captures among 1,377 bats of 15 species) in surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

Utah**:** Long-eared myotis ranked second in relative abundance of 15 species (75 captures among 572 individuals) in the Henry Mountains of southeastern Utah, where elevations of capture sites where this species was taken ranged from 1,433 to 2,713 meters (Mollhagen and Bogan, 1997). In contrast, at Arch Canyon on the Colorado Plateau in southeastern Utah these bats were among the least abundant species, with two bats captured among 295 bats of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016).

Wyoming**:** Long-eared myotis ranked second of seven species (23 of 112 individuals) captured in late summer-early autumn 2010–2011 by mist netting over water at elevations ranging from 1,568 to 3,116 meters in lodgepole pine, Engelmann spruce, subalpine fir, and Rocky Mountain juniper forests with open sagebrush and grassland habitats on the northern range in Yellowstone National Park, Wyoming (Johnson et al., 2017). During 2012 they ranked highest among 12 species (162 captured among about 370 individuals) documented by mist netting in lower elevation basin and foothills habitat in the south-central part of Wyoming (Abernethy et al., 2013). They were low in relative abundance (five among 246 bats of six species, ranking fifth) of bats captured in mist net surveys over streams and beaver ponds in and near the Medicine Bow National Forest in southern Wyoming, at elevations ranging from 2,133 to 2,896 meters and in habitats encompassing lodgepole pine (*Pinus contorta*) and spruce-fir forests (Gruver, 2002).

Elevational Differences in Habitats among Sex and Age Classes: A higher proportion of males were found at elevations greater than 2,311 meters (65%) than below 2,165 meters (15%) in a sample of 270 long-eared myotis from Mesa Verde National Park in southwestern Colorado (O'Shea et al., 2011a). Sex ratios were equal in a sample of 218 adults captured at elevations ranging from 1,350 to 2,150 meters in predominantly lodgepole pine forests in and around the Kananaskis Valley, Alberta, Canada (Barclay, 1991).

FORAGING AND DIETARY ANALYSIS.— In red fir (*Abies magnifica*) – lodgepole pine forests in the Sierra Nevada of California, foraging individuals have been described as flying in straight courses in open spaces about 12 meters above ground during early evening, hunting closer to the ground later in the evening (Ingles, 1949). In coniferous forests (predominantly lodgepole pine) of the Rocky Mountains in Alberta, long-eared myotis foraged mostly along paths through or within the forest (Barclay, 1991). Activity areas of foraging *M. evotis* radio tracked in the western Cascades of Oregon averaged 38 ha, were a mean distance of 518 meters from the day roosts, and were significantly closer to water than random points (Waldien and Hayes, 2001).

Reproductive females studied among cottonwood groves along the Saskatchewan River Valley in Alberta foraged nearly all night long every night with little night roosting, regardless of seasonal differences in the length of darkness, suggestive of narrow energy budgets (Chruszcz and

Barclay, 2003). Foraging activity (as measured by echolocation detectors) in forests of southwestern British Columbia was positively associated with habitat type, forest stand age, and ambient temperature (Luszcz and Barclay, 2016). Black cottonwood (*Populus trichocarpa*) and coastal western hemlock forests had greater activity of this species than Douglas fir and Engelmann spruce-subalpine fir zones in the British Columbia study, with activity higher in old and mature-age forests than in young forests and higher in warmer temperatures; activity also differed between the two years of study with no obvious causal relationships (Luszcz and Barclay, 2016).

Long-eared myotis were long suspected to include gleaning in their mode of foraging (Manning and Jones, 1989), and in captivity often hovered and gleaned prey from surfaces (Barclay, 1991). They have been described as having a flexible foraging strategy (Barclay, 1991). Experimental studies indicated that they relied on prey-generated sounds much more than they used echolocation for detecting and attacking insects while gleaning. In contrast, they consistently used echolocation when aerial hawking, and physical characteristics of echolocation sounds varied between the two hunting strategies (Faure et al., 1990; Faure and Barclay, 1992, 1994).

In several forest types in northern Idaho long-eared myotis have been reported to have the most diverse diet of the five species of bats studied, primarily eating moths but also consuming insects in nine other orders as well as spiders and ticks (Lacki et al., 2007). These bats were categorized as beetle strategists and between, within, and below-canopy foragers based on dietary analysis of bats sampled in the San Mateo Mountains of New Mexico (Black, 1974). However, in lodgepole pine forest of Alberta they ate primarily lepidopterans, and to a lesser degree also consumed hymenopterans, neuropterans, and dipterans (Barclay, 1991). Dietary analysis and skull and jaw morphology indicate that this species may rely more on beetles than moths in areas where they overlap in habitat with the southwestern myotis (*Myotis auriculus*), thought to be a greater specialist on moths (Husar, 1976; Gannon and Rácz, 2006).

Lepidopterans were the most prominent food item observed in guano of long-eared myotis captured at riparian habitats in the Oregon Coast Range, followed by spiders, coleopterans, hemipterans, and other groups (Ober and Hayes, 2008). In northeastern Oregon, they were reported to eat primarily lepidopterans followed by coleopterans (Whitaker et al., 1981). Lepidopterans and coleopterans were the most often encountered groups seen in dietary analysis of fecal samples from northern Arizona ponderosa pine forest, where homopterans were also taken opportunistically (Warner, 1985). In mountains of northern New Mexico, individuals fed on lepidopterans and beetles but consumed mainly beetles at sites where it was sympatric with the morphologically similar southwestern myotis (Husar, 1976). Dietary analysis of stomach contents from northwestern Colorado indicated that coleopterans, trichopterans, and hymenopterans were equal dietary components, followed by lepidopterans in percentage frequency, with other groups of insects each constituting less than 10% (Armstrong et al., 1994). In Douglas fir forests of southern British Columbia, the diet was primarily coleopterans, followed by neuropterans in descending order of percent volume, with lesser amounts of other groups, including caterpillars taken during a spruce budworm (*Choristoneura occidentalis*) outbreak (Wilson and Barclay, 2006). Stomach contents of three individuals from southeastern Montana contained homopterans (cicadellids), dipterans, lepidopterans, odonates, and coleopterans (Jones et al., 1973).

Long-eared myotis were among the species group sampled by Adams et al. (2003) that more frequently drank at watering places with higher concentrations of calcium and other minerals, perhaps providing a supplement to dietary intake that would be most critical to reproductive females and weaned volant juveniles.

ROOSTING HABITS.— Long-eared myotis roost near the ground during warm seasons, using rock crevices, snags, logs, stumps, and living trees. They occupy roosts in very small groups or solitarily, switching among many roosts at a nearly daily frequency. Studies using radio telemetry to locate roosts have emphasized females as described below, but two males were observed roosting in a small fissure in a cliff face in southeastern Montana (Jones et al., 1973), one was found roosting under bark of a tree in southern British Columbia, and nine were found roosting under bark of tree stumps in the same region (Vonhof and Barclay, 1996, 1997).

Winter Roosts: Winter roosts of long-eared myotis are not well known, although they were among the species of bats reportedly found most commonly in surveys of inactive mines (presumably including winter) in Colorado (Navo et al., 2000). In Washington and Oregon, these bats were infrequently encountered hibernating during intensive searches of 650 caves or mines during winters 1982–1989, with just four solitary bats found roosting at three caves (Perkins et al., 1990). Two solitary individuals were reported from another cave near Mount St. Helens, Washington (Senger et al., 1974), and two bats were reported hibernating in a mine in northeastern Montana (Swenson and Shanks, 1979). One record of an apparently hibernating long-eared myotis was from a garage in Corvallis, Oregon during December (Perkins et al., 1990). Three limestone caves in northern California had one to five hibernating individuals in each (Marcot, 1984). Bridges were used as winter roosts of this species in the central Sierra Nevada of California (elevations greater than 1,000 m; Pierson et al., 2001). No bats of this species were observed hibernating in abandoned mines in the White and Inyo Mountains of California and Nevada (Szewczak et al., 1998).

Long-eared myotis occasionally leave hibernacula during winter: Lausen and Barclay (2006) detected echolocation calls of flying bats of this species during winter in the arid prairies of southern Alberta, an area devoid of significant caves. Small numbers were captured in mist nets at the mouth of Azure Cave at 1,361 meters elevation in Montana during September (Hendricks et al., 2000).

Given the lack of extensive records of long-eared myotis hibernating in caves or mines in significant numbers and their propensity to roost in crevices and crevice-like situations in warm seasons (see below), we suspect that in many areas these bats hibernate in small numbers in deep rock crevices, similar to big brown bats in western North America (Lausen and Barclay, 2006; Neubaum et al., 2006; Klüg-Baerwald et al., 2017) and as was postulated for western bats in general by Twente (1960). Those captured and radio tagged in early autumn in Yellowstone National Park roosted in ground-level rock crevices in rock fields or in crevices in lower canyon walls until tags no longer functioned (Johnson et al., 2017).

Warm Season Roosts in Rock and Soil Crevices and Cavities: Rock crevices were the preferred roosts of reproductive females in the piñon-juniper woodlands of Mesa Verde National Park in southwestern Colorado (Snider et al., 2013). Radio tracking of 15 females led to discovery of 33 roosts in rock crevices and one roost in a juniper snag, with roosts less than 2 meters above ground level. These bats roosted in small groups of three or fewer and switched roosts frequently, with an average distance of 424 meters (range 31–1,427 meters) between successive roosts. Despite extensive areas of recently burned forest, all but two roosts were in unburned habitat; occupied rock crevices were on average 118 centimeters higher and 24 centimeters deeper than unoccupied, randomly chosen rock crevices (Snider et al., 2013). On the landscape scale, distance to nearest water and distance to burned habitat were the most important variables related to roost use by long-eared myotis at Mesa Verde National Park, with occupied roosts on average 1,251 meters closer to water and 345 meters farther from burned habitat than unoccupied crevices. Ten roosts found by radio tracking three individuals in the Jemez Mountains of New Mexico ranged 1,585 to 2,542 meters in elevation and were 0.3 to 1.0 kilometers from the point of capture, with five roosts of adult females in rock crevices, and five roosts used over an eight-day period by the single male including both snags and rock crevices; rock crevices utilized as roosts were on or near the ground (Bogan et al., 1998).

On Turnbull National Wildlife Refuge in northeastern Washington (where predominant habitats were ponderosa pine and Palouse zone shrub-steppeland and meadows), 14 reproductive females were tracked to 35 roosts and mean colony size was four bats (Rancourt et al., 2005). All roosts but one were located in two-centimeter-wide crevices in small isolated rocks or basalt cliffs, the exception being a roost under bark in a snag used for one day (Rancourt et al., 2005). Bats switched roosts about every two days, with an average of 149 meters between roosts. Compared to randomly selected plots, habitats immediately around roosts were characterized as open and rocky and not close to permanent water; at a 78 hectares plot size, landscapes at roosting sites were in areas with more grassland and aspen habitat and lower proportions of wetlands (Rancourt et al., 2005).

Roosting of long-eared myotis was intensively studied in both mountain and prairie habitats of southern Alberta, Canada (Chruszcz and Barclay, 2002, Solick and Barclay, 2006a, 2006b, 2007; Nixon et al., 2009). On the prairie, bats roosted most frequently in crevices in boulders and rocks on or near the ground and used torpor on a regular basis, with most adult females roosting solitarily but a few roosting in twos or threes (Chruszcz and Barclay, 2002). Females that were pregnant tended to occupy horizontal rock crevices and used deep torpor more often than lactating females, which tended to roost in vertically oriented rock crevices. These differences in crevice orientation presumably reflect female choice of roosts with thermal conditions suited to their particular energy needs (Chruszcz and Barclay, 2002). In the Rocky Mountains of southern Alberta, they roosted in rock crevices (most vertically oriented) near the ground (81% were on or under the ground surface, with the remainder less than one meter above ground) in rock fields on south-facing slopes (73 of 79 roosts were in rock crevices, six were in snags), with 92% of rock roosts used just once (Solick and Barclay, 2006b). Each female used a roost for an average of 1.2 consecutive days, with average distances between roosts about 50 m. Non-reproductive females entered deep torpor more frequently than pregnant and lactating females. Crevices used by reproductive females tended to be above ground level and passively warmed more quickly than subterranean sites used by non-reproductive females. Pregnant females tended to roost alone, whereas lactating females were more likely to aggregate in roosts (mean group size of three), presumably to raise roost temperatures because warmer crevices were not available (Solick and Barclay, 2006b, 2007). In comparing the roosting ecology of this species in the mountains versus prairies of southern Alberta, Solick and Barclay (2007) observed that reproductive females on the prairie used torpor more frequently than their counterparts in the mountains and that those in the mountains tended to roost in warmer rock crevices exposed to the sun. More frequent use of torpor by the prairie bats may have been related to the longer season of favorable conditions for growth and development of young, or to the need to conserve water in hotter and drier conditions (Solick and Barclay, 2007).

Bats roosting in the badlands habitat of the Red Deer River Valley in prairies of Alberta also switched roosts frequently, regardless of sex or reproductive status (Nixon et al., 2009). Forty-eight bats were tracked to 254 roosts during three summers; all but two of the roosts (one in a rock crevice, one in a shed) were in sheltered erosion cavities and channels in the ground on slopes of river and creek valleys. Regardless of sex or reproductive state nearly all bats roosted solitarily, and roost fidelity was low, with bats switching roosts every one to two days at distances between roosts ranging one to 812 meters (mean 61 m; Nixon et al., 2009). Roosts for most individuals were within areas less than two hectares in size, with one male's roosting area encompassing 4.7 ha, and one lactating female's roosting area only 0.08 ha; roosting areas were broadly overlapping among individuals (Nixon et al., 2009).

Warm Season Roosts in Trees, Snags, and Stumps: In addition to roosting in rock crevices and erosion cavities, long-eared myotis also roost in snags, stumps, and under bark of trees (for example, Vonhof and Barclay, 1996, 1997; Waldien et al., 2000; Arnett and Hayes, 2009). In the western hemlock zone of the western Cascades of Oregon, Waldien et al. (2000) located 73 roosts of 21 radio-tagged reproductive females and determined characteristics of roost trees and the forest stands in which they occurred. Bats were tracked to several types of structures and were found roosting in stumps, snags, trees, and logs in descending order of use. Roost switching was frequent, with occupancy averaging 1.2 days (range one to four). Most adult females were solitary, although groups of up to 14 were observed. Type of roost used did not vary by reproductive condition, and individuals switched among roosts of different structural types (Waldien et al., 2000). Characteristics of roosts in a mature (trees greater than 80 years old), largely unharvested watershed were compared with those in two younger, intensively harvested watersheds. Bats tended to roost in snags in older forests and in stumps in younger forests. Roost sites were not significantly closer to available water than random sites. Most (18 of 20) roosts in snags were in large-diameter Douglas firs, the dominant species of overstory tree in the region. Use of snags in intermediate stages of decay predominated, and snags were more likely to be used if they were close to other snags in intermediate stages of decay (Waldien et al., 2000). (Snags in intermediate stages of decay provide greater opportunities to roost under exfoliating bark or in secondary cavities than those in earlier or more advanced stages.) Snags located farther from stand edges were less likely to be used as roosts. Snags with roosts did not protrude above the surrounding canopy, but their locations in gaps in the canopy and near edges probably offered similar benefits of increased exposure to solar radiation (Waldien et al., 2000). In the harvested watersheds, this species roosted exclusively in crevices in stumps (defined as less than three meters in height), primarily stumps of Douglas fir. Taller stumps were more likely to be used than shorter stumps, as were stumps that were more accessible (less woody debris or vegetation in the immediate surroundings).

In a second study of long-eared myotis roost use in Douglas fir forests of western Washington and Oregon, Arnett (2007) and Arnett and Hayes (2009) augmented the observations by Waldien et al. (2000), especially regarding use of snags. Twenty-seven individuals were radio tracked from one to 15 days each, with individuals using one to seven unique roosts and switching roosts from zero to seven times (Arnett and Hayes, 2009). Both male and female *M. evotis* used snags, downed logs, and stumps that tended to be close (less than one kilometer) to water (88% were within 915 meters of capture sites over ponds). Differences were not observed between sexes in roost use, and use of snags was nearly twice as high in stands with abundant snags (Arnett, 2007; Arnett and Hayes, 2009). Used snags were in stands that did not differ in age from randomly selected stands. Douglas fir snags were used more frequently than other species, but no more than their typical frequency among randomly chosen snags. Use of stumps and logs as roosts was higher in stands with lower densities of snags (Arnett and Hayes, 2009). These results suggest that snags may be preferred roosts of these bats in coniferous forests of their study area in the Pacific Northwest, but that they exploit stumps and logs when snags are less available.

In forests of British Columbia, long-eared myotis roosted in cavities under loose bark of stumps of ponderosa and lodgepole pines in clear-cut areas (Vonhof and Barclay, 1997). Nineteen roosts were found in 17 stumps (among 1,542 examined stumps) located in three of 11 searched clear-cuts and were occupied nearly exclusively by males and non-reproductive or post-lactating females. Clear-cuts with stumps used as roosts generally had less cover (downed logs and vegetation) over stumps, and stumps tended to face southerly directions; these and additional characteristics of roosts suggested that both thermal/metabolic advantages and predator avoidance were likely factors of importance in stump-roosting by this species (Vonhof and Barclay, 1997).

In Yosemite National Park in the California Sierra Nevada Range, long-eared myotis (including a maternity colony) were discovered using basal hollows of giant sequoia trees as roosts during summer (Pierson et al., 2006).

Adult females were radio tracked to 44 roosts in ponderosa pine dominated forests in northern Arizona: 14 in cracks in rocks on the ground, 24 in ponderosa pine snags, four in Gambel oak cavities or snags, and two in downed logs (Rabe et al., 1998a). Three long-eared myotis females radio tracked in east-central Arizona ponderosa pine forest roosted in one ponderosa pine and two southwestern white pine (*Pinus strobiformis*) snags, with two exit counts of 5–6 bats observed (Saunders, 2015).

In piñon-juniper woodlands of the Gallinas Mountains of New Mexico, Chung-MacCoubrey (1996) found a maternity colony of five females roosting in a cavity in the dead trunk of a live juniper. Lactating females radio tagged in late July and early August did not roost in colonies but changed roosts daily, moving among live and dead junipers (primarily *Juniperus monosperma*) and roosting within the twisted folds of trunks. Year-to-year reuse of roosts in trees was documented (Chung-MacCoubrey, 2003).

Warm Season Roosts in Buildings: Reports of non-winter use of buildings as roosts by long-eared myotis are uncommon. Apparently solitary individuals have been reported to roost in cracks or among rafters of buildings on Santa Cruz and Santa Catalina islands, California (von Bloeker, 1967). They have been observed roosting in an abandoned ranch house in Routt County, Colorado, and apparently night roosting in other buildings in the state (Cary, 1911; Warren, 1942). A pregnant female in southern Alberta roosted in a shed for two days but otherwise used natural erosion cavities and channels in the ground (Nixon et al., 2009).

Night Roosts: Long-eared myotis do not seem to use night roosts to a major degree. However, they have been reported night-roosting in an abandoned shed in northwestern South Dakota (Andersen and Jones, 1971), and low numbers of this species were reported to utilize bridges as night roosts in the proximity of the upper Sacramento River in California (Pierson et al., 1996b). Reproductive females studied in Alberta, Canada spent most of the night foraging, roosting for only a small proportion of each night (Chruszcz and Barclay, 2003). In contrast, Albright (1959) reported them to be the most common night roosting bat (predominantly males) at a cave at Oregon Caves National Monument, especially during August.

Population Ecology.— **Litter Size, Natality, and Female Reproduction:** Typical litter size appears to be one. One female long-eared myotis taken in California had a single embryo (Grinnell, 1918), as did two females taken in mountains in southern Nevada (Burt, 1934; Deacon et al., 1964), five females from northwestern South Dakota (Jones and Genoways, 1967; Andersen and Jones, 1971), and a female from the Chiricahua Mountains of southeastern Arizona (Cockrum and Ordway, 1959). Two females with one embryo each were collected in the San Gabriel Mountains of southern California (Vaughan, 1954), and in southeastern Montana (Jones et al., 1973). Cockrum (1955) summarized records for six other females from multiple locations, each with single embryos or young.

Natality rates of long-eared myotis are variable and can be biased by place of capture. Seven of seven females (100%) taken from a maternity colony in British Columbia were all pregnant (Munro and Cowan, 1944). Natality estimates based on captures at watering sites, foraging places, and flyways are lower. Reproductive rates of adult female *M. evotis* in southwestern Colorado varied with the amount of spring precipitation, averaging 34% (32 females) during the 2006 drought year and 69% (42 females) the following year when spring precipitation was higher and insect abundance showed a corresponding increase (Snider, 2009; O’Shea et al., 2011a). Four of six (66%) long-eared myotis taken at Mesa Verde National Park in early June 1989–1994 were pregnant (Chung-MacCoubrey and Bogan, 2003). Two of eight adult females (25%) captured during summer over water in west-central Nevada were reproductive (Kuenzi et al., 1999).

A female reproductive rate of 55% (21 of 38 bats) during summers 1987 and 1988 was found in long-eared myotis captured in coniferous forests (predominantly lodgepole pine) of the Rocky Mountains in southwestern Alberta (Barclay, 1991). Twenty-three of 34 adult females (68%) captured foraging in 2002 in the foothills in the same region were reproductive (Solick and Barclay, 2006b). In prairie badlands of southern Alberta, overall reproductive rates of 77 adult females captured away from roosts during the lactation period in summers 2001–2005 was 57% (Lausen, 2007).

Fifty of 93 (54%) adult females captured in northern Arizona ponderosa pine forests were reproductive during summers 1993–1995, whereas 18 of 23 (78%) were reproductive in northern Arizona pine-oak forests during summers 1994–1995 (Morrell et al., 1999). Bogan et al. (1998) reported ten of 23 (44%) females examined in the Jemez Mountains in New Mexico as reproductive in 1995 to 1997; C. Jones (1964) found 10 of 20 females (50%) netted over water in the Mogollon Mountains in New Mexico and Arizona to be reproductive during the months of June and July 1957 to 1960. Geluso and Geluso (2012) reported a reproductive rate of 92% in 207 adult females captured over water in 19 years of netting at a pond in coniferous forest at 2,573 meters elevation in the San Mateo Mountains of New Mexico. During 1995–1999 in the Cibola National Forest of New Mexico, the ratio of reproductive females to non-reproductive females sampled in ponderosa pine forests of the San Mateo Mountains was 0.94, whereas this ratio was 2.73 in the lower elevation piñon-juniper woodlands of the nearby Gallinas Mountains (Chung-MacCoubrey, 2005). A crude estimate of overall natality based on the cumulative totals of non-reproductive females and reproductive females captured over water across all years and studies is 68% (412 of 603 bats).

Data concerning other demographic aspects of female reproduction such as age at first reproduction and inter-birth intervals are not available in the published literature.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Long-eared myotis are subject to fatal rabies infections (for example, Constantine, 1979; Armstrong et al., 1994; Pape et al., 1999; Bogan and Cryan, 2000; Mondul et al., 2003; Blanton et al., 2007). Helminths, coccidial protozoans, and ectoparasites also have been detected in this species (Whitaker and Wilson, 1974; Rausch 1975; Duszynski et al., 1999; Lausen, 2005), but impact of these infections on mortality of these bats has not been determined. The presence of alpha-coronavirus RNA was detected in 2% of a sample of 52 seemingly healthy individuals netted over water in Colorado, but the significance of these viruses as possible mortality factors remains unknown (Osborne et al., 2011). White-nose syndrome has not been reported for long-eared myotis. Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with antifungal properties on wings of this species and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America.

Deaths of long-eared myotis due to entrapment in oil sludge pits in northwestern Colorado have been reported, as have deaths due to entrapment in water troughs (Finley et al., 1983). Residues of DDT and metabolites in *M. evotis* in Oregon following a forest-spraying showed no appreciable accumulation and no evidence for mortality (Henny et al., 1982). Maximum reported longevity is 22 years (Tuttle and Stevenson, 1982).

Population Trend: Geluso and Geluso (2012) reported an apparent increase in abundance (based on numbers of bats captured) of long-eared myotis over a 34-year period at a pond in the San Mateo Mountains of New Mexico, after adjusting captures for variation in precipitation and year.

Weller (2008) evaluated sampling design considerations for use of occupancy estimation models to assess population status and habitat associations of long-eared myotis in the Pacific Northwest. Occupancy was determined using captures in mist nets and echolocation recordings during four surveys at 51 carefully selected sites in Washington, Oregon, and northern California, and estimated based on a series of habitat models (including successional stage and conservation reserve categories) that were ranked using Akaike's Information Criteria. Long-eared myotis were detected at 26 sites (observed occupancy of 0.509). Model-averaged detection probability estimates were 0.239 ± 0.06 (SE), the lowest of eight species sampled, and overall occupancy estimates were 0.782 ± 0.19 (SE) using the best-ranking model. Point estimates of occupancy were higher in late succession/old growth habitat (Weller, 2008). Increased precision would have been possible with greater numbers of surveys per site and greater numbers of sites, or perhaps by increasing capture success or the number of recorded echolocation calls that are identifiable to species (Weller, 2008).

Species dynamic distribution models were constructed using Bayesian hierarchical modeling techniques for 12 species of bats in Washington and Oregon based on an eight-year monitoring program; bat activity was sampled with mist nets and acoustic detectors, and the analysis accounted for detectability and annual turnover in bat occurrence (Rodhouse et al., 2015). This species did not show a decline in occurrence probabilities with time (Rodhouse et al., 2015).

Management Practices and Concerns.— Waldien et al. (2000) and Arnett and Hayes (2009) recommended the following management practices for maintaining roosting habitat of long-eared myotis and some other species of bats in the western Cascades of Oregon and Washington. Forest management should emphasize maintaining large-diameter conifer snags in early to intermediate stages of decay that are easily accessed by bats. Snags should be exposed to moderate to high levels of solar radiation by protruding above the canopy, or having lower canopy closure or being situated near gaps and edges. Snags should be retained in clusters, particularly where they are in upland habitats near water. Retention of large green trees and snag creation should be practiced, and management should maintain remnant patches of structurally diverse and typically older forest stands (for example, greater than 40 years old) with large snags (Waldien et al., 2000; Arnett and Hayes, 2009). Thinning of densely stocked stands to accelerate development of large-diameter trees for future roosts, and creation of gaps to increase solar radiation were also recommended. Although use of stumps as roosts for this species is important in younger stands, stumps are viewed as more ephemeral and less valuable sites for roosts than snags. This is because the more recently cut stumps do not provide roosts in early years (bark has not exfoliated) and are soon made less accessible or shaded as successional vegetation develops. However, the latter can be ameliorated by removal of vegetation around stumps, particularly those in natural openings and on steeper slopes (Waldien et al., 2000).

Long-eared myotis will use artificial roosts constructed to mimic exfoliating bark on snags in ponderosa pine forests in northern Arizona, including maternity groups of at least seven bats (Chambers et al., 2002; Mering and Chambers, 2012). In studies of several species of bats (including this species) roosting under loose bark or in lightning-caused cracks in ponderosa pine snags in northern Arizona, Rabe et al. (1998a) recommended measures to help recruit snags with loose bark as bat roosts. They suggested that forest management should retain large trees that die in place, thin stands of small trees to allow faster development of larger trees, and kill live large trees in areas of low snag density to hasten roost development. Prescribed fire but with protection of existing snags also may help promote development of future snags (Rabe et al., 1998a).

Myotis leibii — Eastern small-footed myotis (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Rounded Global Status G4, Apparently Secure.

State Designations: Alabama Department of Conservation and Natural Resources (2015a,b): Priority 1 Species of Greatest Conservation Need, Highest Conservation Concern. Arkansas Game and Fish Commission (Fowler, 2015): Species of Greatest Conservation Need. Connecticut Department of Energy and Environmental Protection (2015): State Endangered. Delaware Division of Fish and Wildlife (2006, 2015): Species of Greatest Conservation Need Tier I. District of Columbia (2006, 2015): Species of Greatest Conservation Need Tier 1. Georgia Department of Natural Resources (2015): High Priority Species. Illinois Department of Natural Resources (2015): Threatened. Indiana Department of Natural Resources (2015): Special Concern. Kentucky Department of Fish and Wildlife Resources (2013): Species of Greatest Conservation Need. Maine Department of Inland Fisheries and Wildlife (2016): State Endangered. Missouri Department of Conservation (2016): Species of Conservation Concern, Imperiled. Maryland Department of Natural Resources (2005, 2010, 2016): State Endangered, Species of Greatest Conservation Need. Massachusetts Division of Fisheries and Wildlife (2015): State Endangered. New Hampshire Fish and Game Department (2015): State Endangered. New Jersey Department of Environmental Protection (2008): Species of Conservation Concern. New York Department of Environmental Conservation (2015a,b): Species of Special Concern, Species of Greatest Conservation Need. North Carolina Wildlife Resources Commission (2014): Special Concern Species. Ohio Department of Natural Resources Division of Wildlife (2015): Species of Concern. Oklahoma Department of Wildlife Conservation (2005, 2016): Species of Greatest Conservation Need Tier II, III. Pennsylvania Game Commission (2015): State Threatened. Rhode Island Division of Fish and Wildlife (2015): Species of Greatest Conservation Need. South Carolina Department of Natural Resources (2005, 2015): State Threatened, Species of Greatest Conservation Need Highest Priority. Tennessee Wildlife Resources Agency (2005, 2015): Tier I Species of Greatest Conservation Need. Vermont Fish and Wildlife Department (2015): State Threatened. Virginia Department of Game and Inland Fisheries (2005, 2015b): Species of Greatest Conservation Need, Tier I. West Virginia Division of Natural Resources (2015): Priority1 Species of Greatest Conservation Need.

DESCRIPTION.— The eastern small-footed myotis (Fig. 27) is the smallest myotis found within its distribution, with forearm lengths averaging 32.2 ± 0.78 (SD) millimeters, proportionally small hind feet eight millimeters or less in length, and a body mass of about three to seven grams; its pelage is varying shades of glossy brown, with a blackish face mask, ears, and wing-membranes (Van Zyll de Jong, 1984; Best and Jennings, 1997; Bogan, 1999; Johnson et al., 2011; Fig. 27).

DISTRIBUTION AND SYSTEMATICS.— The eastern small-footed myotis occurs in the U.S. from southern Maine southward through western Virginia, western North and South Carolina and northern Georgia, Mississippi, and Arkansas to eastern Oklahoma. The northern limits are southern Quebec and Ontario in Canada eastward through the New England states, New York, Pennsylvania, and most of Ohio, southern Indiana, southern Illinois, and southern Missouri (Fig. 28; Best and Jennings, 1997; Arroyo-Cabrales and Álvarez-Castañeda, 2008).

Literature on this species prior to the late 1960s can be confusing because of changing nomenclature and improved understanding of the species taxonomic status. Miller and Allen (1928) placed the species in the genus *Myotis* as a subspecies of *Myotis subulatus*, correcting Audubon and Bachman's (1842) original placement of it in the Old World genus *Vespertilio* as the species *V. leibii*. The species was known as *M. subulatus* up to the mid-1960s, but this name is no longer valid. Glass and Baker (1965) petitioned the International Commission on Zoological Nomenclature to formally suppress the name "*subulatus*" and provided further details on the more compli-

FIGURE 27. Eastern small-footed myotis, *Myotis leibii* (photo by J. Scott Altenbach).

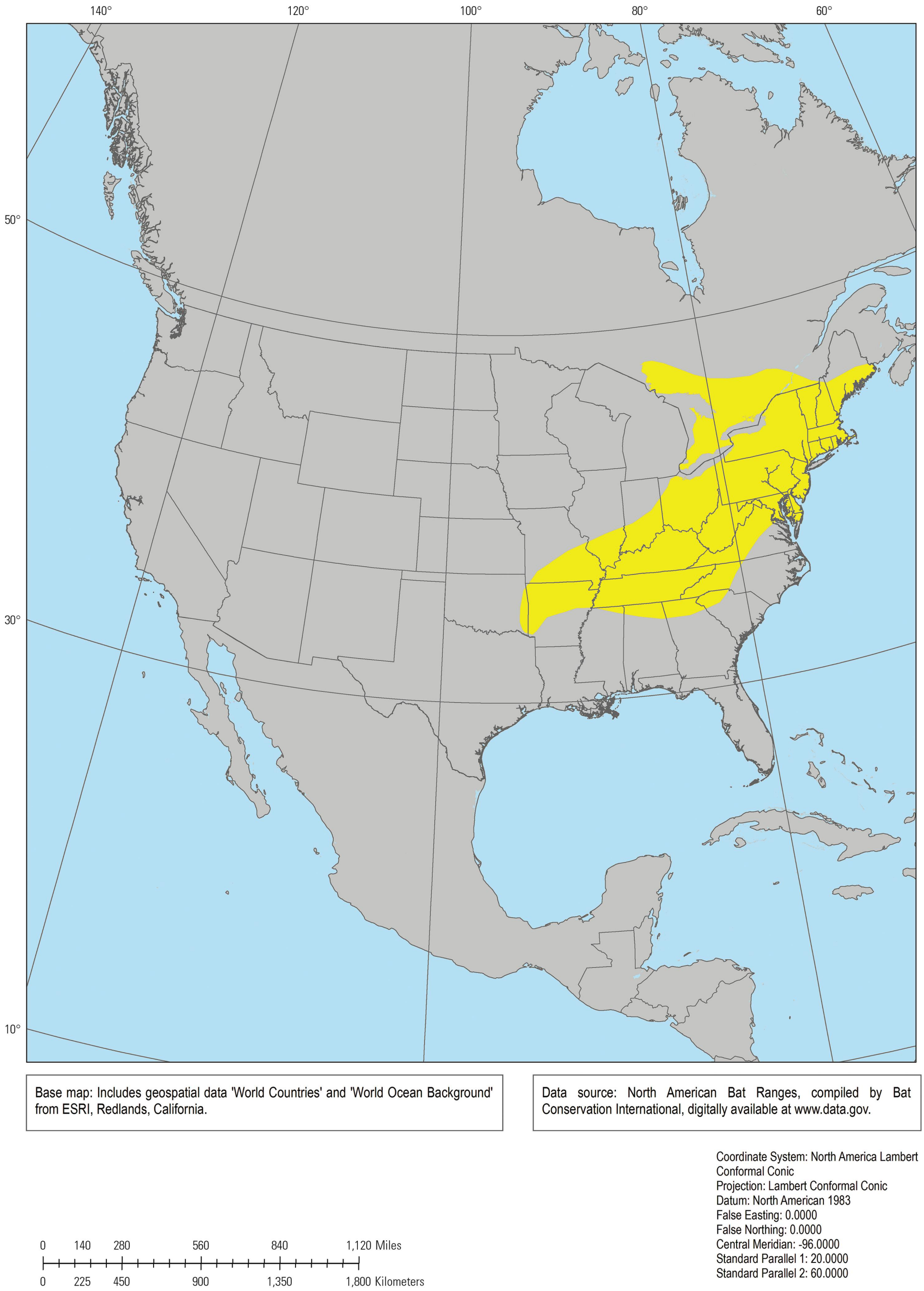
cated taxonomic and nomenclatural history of the species, finally noting withdrawal of the petition and instead correcting the species name to *Myotis leibii* (Glass and Baker, 1968). Morphological analysis of skulls showed clear separation of *M. leibii* from *M. ciliolabrum* (van Zyll de Jong, 1984), which was subsequently supported by protein electrophoretic data (Herd, 1987). Recent molecular genetic analysis also suggests distinctiveness of *M. leibii*, but confirms a close relationship and fairly recent evolutionary separation of *M. leibii* with *M. ciliolabrum* (Rodriguez and Ammerman, 2004; Ammerman et al., 2016).

There are no subspecies of *M. leibii* currently recognized. See Best and Jennings (1997) for a synonymy of past scientific names applied to this species. The generic name originates with Greek words meaning "mouse" and "ear". The specific epithet is a patronym in honor of George Clinton Leib, a 19th Century physician and naturalist, who provided the specimen from Ohio for Audubon and Bachman's (1842) original description of the species. Other common names include eastern small-footed bat, least myotis, least bat, least brown myotis, least brown bat, Leib's myotis, Leib's masked bat, and Leib's bat.

HABITATS AND RELATIVE ABUNDANCE.— The eastern small-footed myotis has mostly been reported from upland forested areas in hilly or mountainous terrain. Habitat associations are poorly known because of the relative rarity of this species, although recent evidence suggests an affinity for talus slopes and other exposed rock outcrops associated with roosting (see below; Johnson and Gates, 2008; Johnson et al., 2011; Whitby et al., 2013; Moosman et al., 2015). Perceived rarity of eastern small-footed myotis in mist netting surveys may be associated with distance to roosting habitat, because probability of capturing them likely drops precipitously with increasing distance from their roost sites (Johnson et al., 2011).

Georgia and South Carolina: Eastern small-footed myotis have only been found in northern parts of Georgia with mountainous or karst topography, representing three of six physiographic provinces: the Blue Ridge, Ridge and Valley, and Cumberland Plateau provinces (Menzel et al., 2000). They ranked lowest in relative abundance (four records) among combined museum and capture records of 1,222 bats of 16 species compiled for the state (Menzel et al., 2000).

Menzel et al. (2003) examined records of all species of bats across the four physiographic provinces of South Carolina, based on 1,002 museum specimens and 2,002 reports of bats captured



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 28. Approximate distribution of the eastern small-footed Myotis, *Myotis leibii*.

during surveys. This species was only found in the Blue Ridge Mountain province of northern South Carolina, and ranked lowest in numbers of specimens (3) and sixth lowest in survey captures (41) among the 14 species documented.

Kentucky and Missouri: Eastern small-footed myotis ranked low in relative abundance among bats captured at the mouth of Colossal Cavern at Mammoth Cave National Park in Kentucky during both spring staging and autumn swarming seasons in 2011–2014; the habitat at the study area is mixed oak-hickory and western mesophytic forest (Lacki et al., 2015). The species ranked fifth in relative abundance, with 19 (1.5%) captures among 1,232 bats of eight species taken in harp traps (Lacki et al., 2015). No eastern small-footed bats were captured in mist nets set over streams during summer at various sites across Missouri during 1977 and 1978, despite the documentation of 1,028 individuals of 10 other species (LaVal and LaVal, 1980).

Maryland and Pennsylvania: Only eight eastern small-footed myotis were captured in the Ridge and Valley physiographic provinces of the central Appalachians of Maryland, mostly in oak forests and at just three of 17 sites in 111 nights of netting during summers 1979–1981; in contrast, a total of 893 bats of four other, more abundant species were captured at all sites combined (Gates et al., 1984). At one of these sites bats were captured at a mine used as a night roost throughout summers 1999 and 2000: eastern small-footed myotis were lowest in relative abundance, with one (1.2%) captured among 81 bats of five species (Agosta et al., 2002). Thirty-one were captured among 2,860 bats of seven species (ranking fifth in relative abundance) in a more extensive sampling at night roosts during summers 1995 and 1996 at seven cave and mine sites in Maryland and western Pennsylvania (Agosta et al., 2005), including five of the same sites in Maryland as in the study by Gates et al. (1984).

In Pennsylvania these bats were found in caves in hemlock forests (*Tsuga canadensis*) at about 600 meters elevation in the central part of the state (Mohr, 1936; Merritt, 1987). They were among the least abundant species captured in mist nets and harp traps set during summer at mouths of caves and mines used primarily as night roosts in the central Appalachian Mountains of Maryland and Pennsylvania (see above; Hall and Brenner, 1968; Gates et al., 1984; Agosta et al., 2002, 2005). Hall and Brenner (1968) netted bats at the mouth of Aitkin Cave in Mifflin County in central Pennsylvania, an area characterized by Appalachian oak forest of the Ridge and Valley physiographic province (Merritt, 1987). Sampling on 17 nights during 1964–1965 resulted in captures of just three (0.2%) individuals among 1,260 bats of five species; just two bats were found during winter hibernation (Hall and Brenner, 1968).

New Hampshire: In Cheshire County, New Hampshire, capture rates in summer ranked second among seven species in an area that was known to be close to diurnal roosts (Moosman et al., 2013). The New Hampshire study area was located in mixed deciduous and coniferous forest and was sampled on 99 nights from 2005–2011 during the progression of white-nose syndrome through the northeastern states: capture rates of this species declined after the initial two years of sampling, consistent with an effect of the disease on bat mortality (Moosman et al., 2013). None were taken in mist-net surveys over water in the White Mountains National Forest of New Hampshire, where 281 bats of six species were captured during 87 nights of netting at 18 sites (Sasse, 1995).

New York: Eastern small-footed myotis were seldom detected in ultrasonic monitoring surveys of bat activity in northern hardwoods habitat, including sugar maple (*Acer saccharum*), American beech, white ash (*Fraxinus americana*), and American elm (*Ulmus americana*; but also including pine and hemlock forests and wetlands) at Fort Drum in New York during 2003–2010 (Ford et al., 2011). This area had historical records of presence and nearby karst formations with likely roosting habitat. Subsequent ultrasonic monitoring at Fort Drum in 2011 and 2012 failed to detect them, perhaps indicating declines attributable to white-nose syndrome (Coleman et al., 2014).

North Carolina and Tennessee: Although relative abundance was not determined, habitats of roosting eastern small-footed myotis were determined for 5 females and 15 males tracked by telemetry in the Unicoi Mountains along the North Carolina-Tennessee border (Thompson, 2013). Roosts were at 913 to 1,441 meters elevation within 70–80 year old hardwood forest with multiple oak species mixed with yellow poplar, American beech, sugar maple, yellow birch (*Betula alleghaniensis*), white pine, and hemlock (Thomson, 2013).

West Virginia and Virginia: In West Virginia, eastern small-footed myotis ranked fifth in relative abundance among 11 species observed during mist-net surveys carried out in 37 counties throughout the state, with 151 (1.3%) bats captured among 11,831 bats taken during summers 1997–2008, prior to the advent of white-nose syndrome (Francl et al., 2012). They ranked seventh after the onset of the disease, with six captures (0.4%) among 1,310 bats taken (Francl et al., 2012). Johnson et al. (2011) found this bat to be the second most abundant species in 50 nights of early summer netting in mixed hardwood, oak-chestnut forest on New Creek Mountain in the Ridge and Valley Physiographic Province of West Virginia, where most were netted over road ruts or ridgetop ponds. Most importantly, they reported that number of captures of this species dropped off sharply when distances between capture sites and talus slopes (where bats roosted) exceeded about 200 meters (Johnson et al., 2011).

Mist-netting surveys over water and roads at 26 sites in western Virginia during summers 1992–1995 resulted in the capture of 11 eastern small-footed myotis, ranking seventh among the 11 species and 235 individual bats documented; most of the eastern small-footed myotis were captured in the Appalachian Plateau physiographic region (Hobson, 1998). In the central Appalachian Mountains of western Virginia, Huth et al. (2015) compared acoustic monitoring with mist netting and visual searches for this species at talus slopes and found acoustic methods to be ineffective, whereas the former two methods used at emergent rock resulted in much higher detection probabilities. They were one of the least abundant species captured during autumn swarming at entrances to 15 caves in western Virginia, with 27 bats taken among 1,452 individuals of eight species during 2008–2013; during winter at these same caves only 10 eastern small-footed myotis were taken among 3,072 bats of seven species (Powers et al., 2015).

FORAGING AND DIETARY ANALYSIS.— Foraging home ranges of four adult female eastern small-footed myotis were determined by short-term radio tracking during spring in western Maryland (Johnson et al., 2009). Minimum home range estimates were 10–100 ha, and maximum distances traveled from diurnal roosts were less than 1.8 kilometers. All bats foraged over the Potomac River, in adjacent riparian forests, and on forested hilltops. The single female located most often foraged closer to paved roads, pastures, coniferous forest, and mixed forest than random locations, with 94% of 74 foraging locations determined to be in forested areas, primarily deciduous forest (Johnson et al., 2009).

Moosman et al. (2007) studied the diet of eastern small-footed myotis during summer in mixed deciduous and coniferous forest in New Hampshire. The diet was diverse, although moths comprised more than half of the diet in their samples. Most food items were categorized as soft or intermediate in hardness, with large, hard-bodied insects such as scarabaeid beetles present only in trace amounts. Diet was similar across demographic groups of bats although juveniles showed evidence of eating proportionally more beetles, and sampling bias may have been involved in this pattern. Presence of non-volant prey (such as spiders and crickets) in the diet led Moosman et al. (2007) to suggest that this species may glean insects from the ground or surfaces of vegetation. Dietary analysis of fecal pellets from 54 individuals sampled during summer in southern New Hampshire also showed lepidopterans composing about half of their prey, followed by coleopterans, dipterans, and arachnids (Thomas et al., 2012).

A diverse diet also was found based on fecal analysis of 44 bats captured during fall swarming at abandoned mine entrances in oak forests of the New River Gorge National River in southern West Virginia (Johnson and Gates, 2007). Lepidopterans were an important component of the diet in autumn at New River Gorge, but six other orders of insects also were found: dipterans, coleopterans, hymenopterans, psocopterans, neuropterans, and hemipterans in decreasing order of proportional volume and frequency (Johnson and Gates, 2007). Additional study of the diet on a larger sample of 77 eastern small-footed myotis in northeastern West Virginia near the Maryland border confirmed the importance of lepidopterans (found in the diet of females more often than in males), followed by coleopterans and dipterans, with lesser proportional frequencies of several other groups (Johnson et al., 2012c).

Roosting Habits.— Winter Roosts: Eastern small-footed myotis are known to hibernate in caves during winter. They are reported to enter hibernacula late in the season and to leave early relative to other species; the species often is found in colder (sometimes at sub-freezing temperatures) and drier areas of caves than other species and may shift locations within a winter, perhaps foraging during warm spells (Mohr, 1936, 1942; Hitchcock, 1949, 1965; Fenton, 1972). At some winter hibernacula they seem to roost primarily alone, with three bats the largest cluster reported in Pennsylvania caves by Mohr (1936); in contrast, a compact cluster of as many as 35 hibernating individuals was reported wedged in a small crevice at a cave in Ontario, Canada (Hitchcock, 1949). Occasionally individuals may hibernate in contact with other species of bats (Fenton, 1972).

In Pennsylvania, Mohr (1942) first observed these bats hibernating in caves in 1931 and subsequently banded 198 out of 272 hibernating at three caves in the central part of the state from 1933 to 1942. He found only one case of a movement between caves, and this was attributable to rock fall at the original hibernaculum (Mohr, 1936, 1942). Mohr (1936) noted that he searched over 100 caves in Pennsylvania and West Virginia for hibernating bats but found eastern small-footed myotis in only seven caves, mainly in central Pennsylvania. Krutzsch (1966) surveyed two Pennsylvania caves during winters 1960–1962 that were previously surveyed by Mohr (1936). He observed one to three individuals clinging to rock walls during each of five visits. In West Virginia, Krutzsch (1966) also surveyed two caves during winter months and observed up to 15 individuals, most scattered along cave walls or in small crevices near the entrances (26 were observed at one cave in early spring). They also have been reported hibernating a short distance inside a cave entrance in Massachusetts (Veilleux, 2007).

Caves used as hibernacula in western Maryland were surveyed during winters 1979–1981 by Gates et al. (1984). Searches of about 49 caves during winter yielded records of just two hibernating eastern small-footed myotis (one each at two caves) compared with 1,087 sightings of four other hibernating species (Gates et al., 1984). Allen (1939) reported them hibernating solitarily and in pairs in small crevices within a cave in Vermont. In New York, they were found hibernating in an old mine beneath fallen rock slabs in three groups: two males, three males, and four males with five females; one to 14 bats were also observed hanging singly from the ceiling at multiple visits during the same winter (Martin et al., 1966). In two other New York mines, solitary bats and groups of up to 30 were observed hanging from ceilings in hibernation, some over water (Martin et al., 1966).

Eastern small-footed myotis have been found roosting on or near cave floors under rocks or in crevices (including one in clay) during winter in West Virginia (Davis, 1955; Krutzsch, 1966), New York (Martin et al., 1966), and Arkansas (McDaniel et al., 1982). Most of these observations were of solitary bats, but a group of nine also was observed (Martin et al., 1966). Tuttle (1964) also reported an individual roosting near the floor of a cave used as a hibernaculum in Tennessee, as well as three hanging solitarily from the ceiling of the same cave. Five (four males, one female) were found hibernating in a dry passage within a cave in Missouri during March 1971, and a single male was found hibernating in the same area of the cave in November 1971 (Gunier and Elder, 1973). Records of use of two caves in Missouri by one and 20 individuals, including some apparent use as hibernacula, were reported by LaVal and LaVal (1980). Single bats also have been taken from hibernacula during winter in mountainous areas of West Virginia (Johnson, 1950; Krutzsch, 1966). Summaries of counts at 42 hibernacula in New York, Pennsylvania, Vermont, Virginia, and West Virginia over multiple years revealed 25 caves used by this species, with total counts in any one hibernaculum ranging from 0 to 721 prior to the advent of white-nose syndrome, and 0 to 485 afterwards (Turner et al., 2011).

In a cave in Renfrew County, Ontario, Hitchcock (1945) counted eastern small-footed myotis seen hibernating in winter from 1942 to 1945 and noted a range of 30–142 bats, about equally divided between males and females. Earlier observations in two other caves in Ontario and Quebec during winter noted only two and four hibernating individuals (Hitchcock, 1941). Over an extended period of 23 years of winter observations at five structurally simple hibernacula in Ontario and Quebec (during which most bats seen were banded), Hitchcock (1965) reported this species as ranking third in abundance, with 626 bats banded compared to 5,236 bats of four other species. The largest reported winter counts at single Ontario caves were 142 individuals in 1944 and 113 bats in 1953 (Hitchcock 1949, 1965; Hitchcock et al., 1984), in contrast to a recent maximum of 721 bats counted at a cave in New York during the year 2000 (Turner et al., 2011). Two maximum records of movements between winter hibernacula and summer colony sites in Ontario were reported to be 16 and 19 kilometers (Hitchcock, 1965).

Griffin (1940) tabulated numbers of hibernating bats banded in caves and mines in New Hampshire, Vermont, Connecticut, Massachusetts, and New York from about 1934–1939: eastern small-footed myotis ranked last among six species, numbering 11 of 11,739 bats banded. It is unknown what biases were involved in choosing individuals to be banded, but these now-historical data may be suggestive of the comparative rarity of this species in the region, or their use of sites other than caves as hibernacula. The latter was suggested as a possibility for northeastern bats in general by Griffin (1945).

Although caves have historically been a research focus as winter hibernacula for eastern small-footed myotis, it has been suggested that they may also choose rock crevices for overwintering (Johnson and Gates, 2008). Saugey et al. (1993:103) speculated that "rock glaciers" or "rock rivers" (talus slopes) might provide winter roosts in Arkansas in the absence of caves. Some species of bats in the western U.S. and Canada are known to use rock crevices as winter hibernacula (Lausen and Barclay, 2006; Neubaum et al., 2006; Klüg-Baerwald et al., 2017). Findings of roosting individuals under rocks and in crevices away from caves during spring and autumn months also may suggest winter hibernation in such situations (see below).

Warm Season Roosts in Crevices, Under Rocks, and in Caves and Tunnels: Roosts of eastern small-footed myotis have been found in crevices in rock outcrops from early spring through autumn. Two individuals were reported roosting under a large flat rock at the edge of a quarry in Tennessee at the end of April (Tuttle, 1964), and a single bat was taken in a cave in western North Carolina in March (Adams, 1950). Up to 26 individuals were observed scattered along walls and in small crevices of a cave used as a hibernaculum in West Virginia in late March and early April 1961 (Krutzsch, 1966). Two (one male, one female) were found roosting together in torpor under a 0.5–meter-diameter sandstone rock on a sheet of exposed sandstone bedrock in early November 2005, the first verified record of the species in Illinois (Steffen et al., 2006). For several years the only record of this species in Missouri was from beneath a stone on a hillside observed during early October 1949 (Barbour and Davis, 1969).

Spring roosting habits were determined for eastern small-footed myotis captured at night during mid-March to mid-May 2007 in an abandoned railroad tunnel within the Chesapeake and Ohio Canal National Historical Park in western Maryland (Johnson and Gates, 2008). Forty-seven bats were captured and individually marked, including four females tracked with radio transmitters for a mean of eight days. These four females all roosted in crevices in rock outcrops on south-facing slopes in shale barrens (consisting of talus slopes and rock outcrops with sparse vegetation), mainly along the Potomac River Gorge less than 1.1 kilometers from the tunnel (Johnson and Gates, 2008). Bats roosted solitarily in these crevices and switched roosts daily to alternate sites within 50 meters of each previous roost. Characteristics of rock outcrops used were similar to randomly selected outcrops (Johnson and Gates, 2008).

A solitary male was found under a rock in early July 1950 in Westmoreland County, Pennsylvania (Doutt et al., 1966). In southern Illinois, Whitby et al. (2013) visually searched 15 exposed sandstone outcrops on the Shawnee National Forest for roosting eastern small-footed myotis during summer 2011. Eight outcrops had roosting bats, with 29 bats observed, mostly solitary but some in groups up to five individuals. Roosting bats included adult females, juveniles, and adult males, and all were found under loose rocks lying on exposed bedrock, none in crevices or under large boulders (Whitby et al., 2013).

Crevices in rock outcrops and cliffs also are used as roosts during summer by solitary males and by reproductive females, the latter sometimes in small groups (Johnson et al., 2011). Five lactating female eastern small-footed myotis and five non-reproductive adult males were radio tracked to 57 roosts on New Creek Mountain in West Virginia over periods ranging four to nine days during June and July 2008. Males and females roosted separately in narrow crevices in rock outcrops on sandstone talus slopes or rock fields within clearings for electricity transmission lines, with 53 roosts (93%) at ground level and four roosts in vertical cliffs (Johnson et al., 2011). Crevice dimensions were about 50 centimeters wide and 39 centimeters deep. Males roosted alone, but females roosted solitarily or in groups of up to eight adults. Individuals of both sexes switched roosts an average of every 1.1 days, with distances between consecutive roosts averaging about 41 meters in males and 66 meters in females (Johnson et al., 2011). Roosts were located in areas with low canopy cover and within 15 meters of shrubs or forest edges, with female roosts closer to upland water sources than male roosts, and all roosts were located downslope at points ranging from 19 to 236 meters from the capture site. Comparisons with randomly selected sites were not made. In New Hampshire, diurnal roosts used during summer were reported in rock outcrops and in boulder riprap covering the face of a dam (Moosman et al., 2013).

Summer roosting habits of radio-tracked eastern small-footed myotis were determined in the Unicoi Mountains along the Tennessee and North Carolina border (Thomson, 2013). Twenty bats were tracked to 17 other roosts from two bridges that provided day roosts in crevices in expansion joints. Two roosts were in white pine snags and 15 roosts in large, south-facing rock-like surfaces or structures, including nine rock crevices in road cuts and other roosts in loose rock in an old quarry, a boulder within a forest, metal guardrails, and a cement retaining wall; most bats observed in crevices in the bridges were solitary males (Thomson, 2013). Bats were tracked from two to 23 days, averaging 2.6 days continuous residency with movements between successive roosts averaging 721 ± 461 (SE) meters (range 19–8,522 meters); most males roosted solitarily (Thomson, 2013).

In the Blue Ridge Mountains of Virginia, Moosman et al. (2015) conducted visual searches for eastern small-footed myotis on talus slopes during 2013 and spring 2014. They found 23 roosts in crevices in and between boulders, including a maternity colony of about 20 bats in a vertical crevice in a three-meter-diameter boulder during July and a second maternity colony of unknown size in a large six by seven meter boulder in a similar area during June. Similar findings were reported from visual searches in the same study area the subsequent summer by Huth et al. (2015), who found 62 bats roosting in rock crevices on talus slopes. A single individual of this species also was reported roosting in the space formed between two stacked rocks on a talus slope at 1,300 meters elevation in Pendleton County, West Virginia near the Virginia border (Roble, 2004).

Warm Season Roosts in Buildings and Bridges: Eastern small-footed myotis will roost in small maternity colonies in buildings during warm seasons, but reports are rare. A colony of about 10–15 bats was found roosting behind a shed door in Ontario during July 1953, one of which had been banded in a cave in winter about 16 kilometers away; another banded individual was found dead outside of a nearby home during the same summer that was 19 kilometers from its hibernaculum (Hitchcock, 1955). Eastern small-footed myotis were reported to form maternity colonies of 12–20 bats in buildings by Merritt (1987; location unspecified).

During searches for roosting bats in 145 buildings in Great Smoky Mountains National Park in Tennessee, this species was found in three structures, including a building occupied by people during the day (Fagan et al., 2016). Two of the three buildings were historic, one of which was occupied by a maternity colony of 17 bats in a rotting porch rafter in mid-June and early July, and the second by two adult females with two volant juveniles roosting at a ceiling-beam juncture in early July; the third building had guano deposits and a single dead bat (Fagan et al., 2016). The three roosts in buildings were in rocky upland terrain at elevations of 601–699 meters in surrounding habitats described as floodplain, oak–hickory, and hardwood cove forest (Fagan et al., 2016). A maternity colony (greater than18 bats) was also reported apparently roosting under cedar shakes on the porch roof of an old cabin in oak-birch-hemlock forest at 1,447 meters elevation in western North Carolina (O'Keefe and LaVoie, 2010).

In addition to buildings, summer roosting of eastern small-footed myotis (including a maternity colony of less than 20 bats) in guardrail crevices and expansion joints in concrete bridges have been reported in Kentucky, North Carolina, South Carolina, and Tennessee (Barbour and Davis, 1974; O'Keefe and LaVoie, 2010; Thomson, 2013), and use of bridges as roosts has been noted in Arkansas (Sasse et al., 2013).

Night Roosts: Eastern small-footed myotis are known to use night roosts, especially at caves and mines, as has been observed in Kentucky, Pennsylvania, and Maryland (Davis et al., 1965; Hall and Brenner, 1968; Agosta et al., 2002, 2005; Johnson and Gates, 2008).

POPULATION ECOLOGY.— **Litter Size, Natality, and Female Reproduction:** Litter size is reported to be one in general accounts (for example, Barbour and Davis, 1969; Whitaker and Hamilton, 1998), but few supporting data are available in the published literature. Natality estimates indicated high rates of reproduction. Three of four adult females captured in mist nets near roosting sites in the Blue Ridge Mountains of Virginia during summer were reproductive (Moosman et al., 2015), 10 of 11 adult females captured at roosts in western North Carolina and eastern Tennessee during summer were reproductive (Thomson, 2013), and each of 22 adult females captured very near a maternity colony in North Carolina during July were reported to be lactating or post-lactating (O'Keefe and LaVoie, 2010). Fifty-nine of 62 adult females (95%) captured during mist-netting surveys in West Virginia were reproductive (Francl et al., 2012; based on captures between dates of June 6 and August 11 in 1998–2010). We are unaware of any published literature with quantitative data concerning other demographic aspects of female reproduction in the eastern small-footed myotis, such as age at first reproduction and inter-birth intervals.

Survival: Hitchcock et al. (1984) provided annual adult survival estimates for eastern small-footed myotis banded at a hibernaculum in Ontario over a seven-year period during the 1940s. Cormack-Jolly-Seber estimates (± SE) were 0.76 ± 0.11 for males and 0.42 ± 0.07 for females. The estimate for females appears unsustainable (see review in O'Shea et al., 2011c), but possibly may include permanent emigration, banding-caused mortality (Hitchcock, 1965; O'Shea et al., 2004), or other unknown effects. Reported maximum longevities for two male and two females banded in Ontario were six to nine years (males) and six to 12 years (females; Hitchcock, 1965).

Mortality Factors: Historically reported mortality factors include commercialization of caves used as hibernacula, scientific collecting (including for rabies research), and banding (Hitchcock, 1965). Mercury concentrations in tissue of seven eastern small-footed myotis from the northeastern United States were similar to those of other species of myotis, big brown bats, and tri-colored bats (*Perimyotis subflavus*), in being higher than in migratory tree bats of the genus *Lasiurus* (Yates et al., 2014). The non-migratory species considered collectively showed age, sex, and site effects for mercury concentrations in blood and hair, and correlations were seen between methyl mercury and total mercury in blood and hair of this group of species; impacts of mercury exposure on mortality in the sampled populations were unknown, but it was speculated that transfer in breast milk might have a negative effect (Yates et al., 2014). Organochlorine compounds were analyzed in tissues of two individuals, but with no link to mortality (Kannan et al., 2010).

Two eastern small-footed myotis were reported crushed behind a sliding shed door in Ontario (Hitchcock, 1955). This species very seldom is reported dead at wind turbines (for example, Arnett et al., 2008; see also O'Shea et al. 2016a), although two deaths at turbines have been reported in Ontario (Jacques Whitford Stantech Ltd, 2009). Rabies occurs in this species (Constantine, 1979). However, they are seldom found or identified in public health samples taken for rabies diagnostic tests, perhaps because of their rarity or their infrequent use of buildings as roosts. For example, Whitaker and Douglas (2006) reported rabies prevalence statistics for 8,262 rabid and non-rabid bats taken over a 38-year period in Indiana, and no eastern small-footed myotis were among the carcasses examined. Similarly, only 32 individuals were found among 30,709 identified bats examined for rabies in the entire United States during 1993–2000 (Mondul et al., 2003).

DNA from the fungus causing white-nose syndrome as well as associated lesions have been reported for the eastern small-footed myotis (Foley et al., 2011), and a summary of changes in counts at 42 caves used as hibernacula showed a drop of 12% (1,303 to 1,142 bats) after the advent of the epizootic, the least reduction of the six species monitored at these sites (Turner et al., 2011). Few have been included in diagnostic reports of multiple mortality events due to white-nose syndrome (for example, see compilations by O'Shea et al., 2016a). However, mist-netting and acoustic surveys in some areas suggest drops in abundance subsequent to arrival of the epizootic (Francl et al., 2012; Moosman et al., 2013; Coleman et al., 2014; see "**Population Trend**" below). Lacki et al. (2015) hypothesized that because these bats are small and have lower fat reserves upon entering hibernation, they may be more subject to loss of energy reserves subsequent to infection by the fungus.

Population Trend: Trombulak et al. (2001) assessed winter counts of all species of hibernating bats at 23 caves and mines used as hibernacula in Vermont, including surveys that began during the 1930s. The eastern small-footed myotis was seldom present at most hibernacula during most surveys, and when present was always at low numbers, such that no conclusions could be drawn about changing status over time (Trombulak et al., 2001). Ellison et al. (2003) analyzed trends in counts for this species at ten hibernacula in Pennsylvania, with counts made in five to 12 winters at each site (data provided by J. Hart of the Pennsylvania Game Commission). No trend was detected at eight sites, and two sites showed an increasing trend; overall, numbers counted were low, ranging from 0 to 46 bats (Ellison et al., 2003). Changes in counts at five hibernacula prior to the white-nose syndrome epizootic indicated positive population growth at four sites, negative at 1, but 95% confidence intervals for trend estimates for this species at all hibernacula included negative growth (Langwig et al., 2012). Sex ratios of bats at winter hibernacula are about 1:1 (Mohr, 1936, 1942; Hitchcock, 1949, 1965; Fenton, 1972).

Acoustic surveys for this species at Fort Drum in New York during active seasons in 2011 and 2012 failed to detect their presence despite a known history of occurrence prior to the advent of white-nose syndrome, perhaps indicating a negative impact of the disease on the population (Coleman et al., 2014). Relative abundance surveys of bat communities in West Virginia prior to and since white-nose syndrome showed a six-fold drop in numbers of these bats captured per mist-net night (Francl et al., 2012). Similarly, capture rates of this species showed a significant drop between samples taken in mist nets early versus later during the epizootic at a study area in New Hampshire (Moosman et al., 2013).

Recent evidence suggests that eastern small-footed myotis may be less restricted to use of caves than was previously appreciated; widespread year-round use of roosts in rock outcrops and talus slopes could strongly bias prior understanding of population size and trend (see “Roosting Habits” above). Therefore Moosman et al. (2015) explored the feasibility of assessing abundance of these bats during summer by netting at talus slopes, visually searching for roosting bats at such areas, and using randomly placed quadrats over talus slopes to obtain an index of local abundance. They conducted field work on talus slopes in the Blue Ridge Mountains of Virginia and used time-constrained searches to visually inspect crevices in rocks and sometimes extracted roosting bats in talus slopes identified through satellite imagery. They also systematically placed mist nets at talus fields and randomly placed circular quadrats over talus areas to estimate density (Moosman et al., 2015). In summer, they discovered 3.1 ± 1.1 (SE) bats per person-search hour, with 27 bats of both sexes discovered (20 solitary, two pairs, and one roost with three) at 23 roosts. Roosting bats were found between mid-March and late October but not during winter searches, when authors speculated the bats might possibly hibernate deeper below the surface of the talus. Thirteen bats or 4.3 ± 2.1 (SE) bats per net-night were captured in the systematically placed nets. Surveys of random quadrats at one 3.0–hectare talus slope revealed six bats in 337 searched crevices, which were scaled up to 48–343 bats (depending on method) in an area with an estimated 8,873–11,018 suitable crevices (Moosman et al., 2015). Subsequent research on these talus slopes compared detection probabilities based on visual searches using belt transects, mist netting, and passive acoustic detection (Huth et al., 2015). Detection probabilities were 0.00 for acoustic sampling, 0.75 for mist netting, and 0.91 for visual searches (Huth et al., 2015).

MANAGEMENT PRACTICES AND CONCERNS.— This species was recently petitioned for listing under the U.S. Endangered Species Act of 1973, primarily because of its apparent rarity, loss or degradation of habitat, threats from white-nose syndrome, as well as other natural and anthropogenic threats and perceived inadequacy of protections (Center for Biological Diversity, 2010; U.S. Fish and Wildlife Service, 2011). The resultant finding was that listing was not warranted because there was no evidence of a concentration of threats in a significant portion of its range, or that its range had been significantly contracted (U.S. Fish and Wildlife Service, 2013b). The recent findings that the eastern small-footed myotis roosts in talus or talus-like areas may warrant more attention for future management.

Myotis occultus — Arizona myotis (Family Vespertilionidae)

CONSERVATION STATUS.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act, as *M. lucifugus occultus*). Bureau of Land Management (2017): Sensitive Species (Arizona state office). International Union for the Conservation of Nature (2017): Least Concern (as *M. occultus*). NatureServe (2017): Rounded Global Status G4, Apparently Secure (as *M. occultus*).

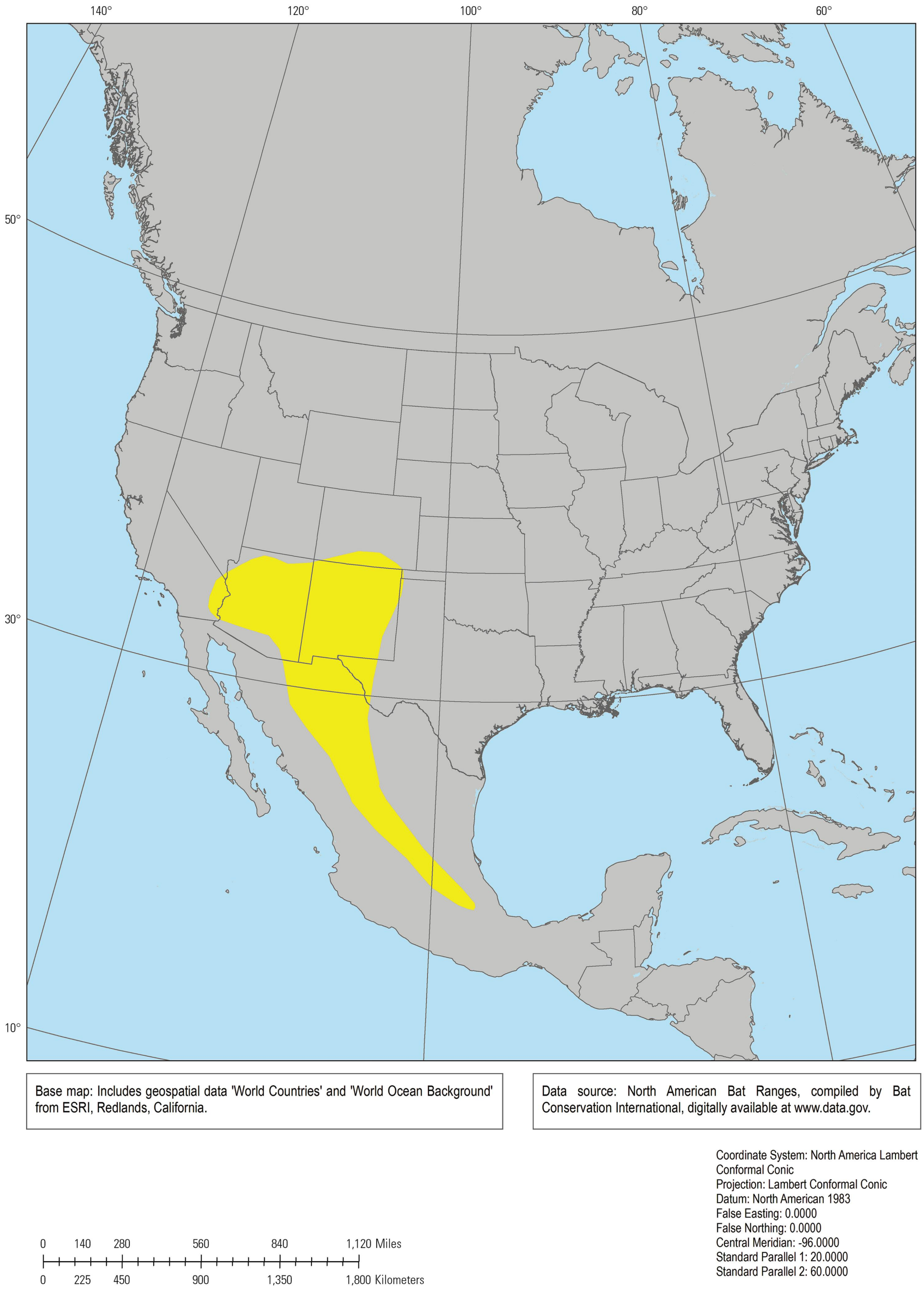
State Designations: Arizona Game and Fish Department (2012): Species of Greatest Conservation Need Tier 1B (as *M. occultus*). California Department of Fish and Wildlife (2017): Special Animals List, Species of Special Concern (as *M. occultus*). New Mexico Department of Game and Fish (2015): Species of Greatest Conservation Need, Sensitive (as *M. occultus*).

FIGURE 29. Arizona myotis, *Myotis occultus* (photo by J. Scott Altenbach).

DESCRIPTION.— The Arizona myotis is a medium-sized myotis, with a body mass of 4–9 g (Ewing et al., 1970; Ammerman et al., 2012a). Mean forearm lengths in various populations range 35.7 to 40.8 millimeters, with an overall mean of 37.9 millimeters (calculated from Findley and Jones, 1967). Overall appearance (Fig. 29) is similar to the little brown myotis (*M. lucifugus*), but often with a reddish or auburn tinge to the dorsal fur and tan or light brown ventral pelage. This species can be distinguished in hand from most sympatric species of myotis because the wing membranes and ears are dark to black in color rather than light-colored as in the slightly smaller and lighter-colored Yuma myotis, and because the calcar is keeled and the underside of the wing membrane is more densely furred in the long-legged myotis (*M. volans*). There is no keel on the calcar of the Arizona myotis, unlike the similarly sized long-legged myotis, and the smaller California myotis and western small-footed myotis. Ear length (about 13 millimeters, range 11–16 millimeters; Hoffmeister, 1986) is typically smaller than long-eared myotis, fringed myotis, and southwestern myotis (*M. auriculus*). The cave myotis (*M. velifer*) is larger and has a sparsely furred region on the back between the shoulders.

DISTRIBUTION AND SYSTEMATICS.— In the United States, the Arizona myotis is found from southwestern and south central Colorado southward, throughout New Mexico and Arizona to southeastern California (Fig. 30) and perhaps extreme western Texas (where only a single record is known; Ammerman et al., 2012a). There are no recognized subspecies. The generic name *Myotis* stems from Greek roots meaning "mouse" and "ear"; the specific epithet *occultus* is Latin for "hidden" or "mysterious". Simmons (2005) uses Arizona myotis as the common name for this species. Other English common names include occult myotis, occult bat, Arizona occult bat, southwestern little brown myotis, occult little brown bat, and Hollister's bat.

The taxonomic status of the Arizona myotis has been in flux because various assessments have been made over the years using increasingly sophisticated methods. The most recent analysis treats the taxon as a full species (Piaggio et al., 2002). This status is recognized by standard mammalian taxonomic authorities such as Simmons (2005) and Bradley et al. (2014). However, some authors remain hesitant about the status of this taxon as a full species (for example, Armstrong et al., 2011; Dewey, 2006). Given past uncertainty and likely confusing expert opinions about the taxonomic status of this species, below we provide a history of the factors influencing past changes to the species nomenclature. The Arizona myotis is an endemic southwestern taxon with regional variation in cranial morphology and dentition, and a complex and only partially understood evolutionary history. Regardless of past debate regarding species status, Piaggio et al. (2002:393) point out that "we think it would be a mistake to assume that if population declines of *M. occultus* occur,



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 30. Approximate distribution of the Arizona myotis, *Myotis occultus*.

they are inconsequential because they merely represent some small portion of the total population of *M. lucifugus*. Our results suggest that declines in *M. occultus* might jeopardize a unique southwestern species."

Discovery and Early Findings: Hollister (1909) described *M. occultus* as a new species based on two specimens shot in flight on 14 May 1905 among cottonwood trees along the west side of the Colorado River, 16 kilometers upstream from Needles, California. Morphologically *M. occultus* was considered distinctive compared to other *Myotis* known at the time in that the skull had a low flat braincase and the rostrum was wide and flat; the specimens also showed reduction or loss of the upper third premolar (Hollister, 1909). J. Grinnell (1914) obtained an additional six specimens shot along the lower Colorado River in California (eight kilometers northeast of Yuma, Arizona) during May 1910, and noted that these also had a broad, flat-topped rostrum and braincase, and that three specimens lacked the upper third premolar, which was also much reduced in the other three specimens. The distinctiveness of these characters was affirmed by H. Grinnell (1918). An additional specimen was obtained in 1920 along the Rio Grande near Las Cruces, New Mexico; this specimen had one minute third premolar on one side of the upper jaw (Allen, 1922). In a subsequent systematic review of all North and South American myotis, Miller and Allen (1928) examined a total of 27 specimens from California, Arizona, New Mexico, and Sinaloa, Mexico, and verified the validity of the species based on the cranial characteristics noted by the previous authors. However, they also presaged later investigations with the comment (Miller and Allen, 1928:24) that "This name is applicable to a peculiar and imperfectly known species inhabiting the southwestern United States and adjoining parts of Mexico." Stager (1943b) examined a further 91 skulls from southern California and confirmed the tendency for loss of the second upper premolar in 62 individuals.

Re-Classifying as a Subspecies and Subsequent Debate: The Arizona myotis was considered a valid species for the next four decades after the work of Miller and Allen (1928), until Findley and Jones (1967) examined a larger sample of *M. occultus* and *M. lucifugus* from the southwestern U.S. and Mexico. They suggested that differences in rostral area between more northern specimens assigned to *M. lucifugus carissima* (65 specimens) and southern specimens assigned to *M. occultus* (260 specimens) were a function of a clinal gradient in overall skull size (length of maxillary tooth row was a correlate of measures of skull size), with northern forms having overall smaller skulls and *M. occultus* showing more variability in skull size (Findley and Jones, 1967). However, they also noted that few specimens were available from geographically intermediate areas to verify this pattern. They remarked that most samples of putative *M. occultus* had "relatively very large teeth" compared to teeth of *M. lucifugus* from northern populations, and that the *occultus* forms have a more prominent sagittal crest and show a reduction in numbers of upper premolars (Findley and Jones, 1967:437), consistent with findings of past authors (Hollister, 1909; Grinnell, 1914; Miller and Allen, 1928). However, based on their overall geographic comparisons of cranial size and rostral area, the authors felt that geographic intergradation was present (but with just four intergrade specimens examined) and stated (Findley and Jones, 1967:438), "We tentatively conclude that *M. occultus* is a large-skulled, large-toothed southwestern race of *M. lucifugus*." On this basis they assigned 260 of the specimens examined from 38 localities as the subspecies *M. lucifugus occultus* rather than as *M. occultus* (Findley and Jones, 1967).

Findley and Jones (1967) [and later Findley et al. (1975)] suggested that populations of the putative subspecies *M. lucifugus occultus* consisted of larger individuals where there was competition with greater numbers of other species of *Myotis* in areas of sympatry. Subsequently, Barbour and Davis (1969) suggested that hybridization rather than intergradation may occur between the two species and suggested that more evidence to support the change from species to subspecies status was needed. They later obtained and examined 189 new specimens (Barbour and Davis, 1970), including 18 bats sampled from geographically intermediate areas in Colorado, and they agreed with the opinion of Findley and Jones (1967) that it was a subspecies based on numbers of premolars and length of the maxillary tooth row.

The subspecies status was later questioned by Findley (1972) who used factor analysis, correlation, and distance analysis to perform a detailed quantitative assessment of 48 mensural characters on 114 species, subspecies, or forms of bats of the genus *Myotis* worldwide. *Myotis occultus* and *M. lucifugus carissima* formed distinct subgroups apart from each other. Factor analysis showed *M. occultus* belonged to a subgroup with *M. grisescens* and five other species, and *M. lucifugus carissima* fell into a different subgroup with five different species (*M. l. carissima* is the subspecies of *M. lucifugus* geographically closest to *M. occultus* to the north); similar separate groupings also appeared in correlation phenograms and distance phenograms (Findley, 1972). At this point, Findley concluded "Either *occultus* is a *lucifugus* which has converged strongly toward the *grisescens* group phenome, or the field relationships of *carissima* and *occultus* have not been fully elucidated" (Findley 1972:43). Harris (1974) speculated on the biogeographic history of the two forms, with alternative interpretations that hinged somewhat on the specific or subspecific status of *M. occultus*.

A contrary view was taken by Hoffmeister (1986) who noted that the supposed intergradation seen by Findley and Jones (1967) was only based on four specimens and very few cranial measurements. Hoffmeister (1986) used as many as 27 cranial measurements and multi-dimensional analyses; based on patterns of morphological separation he concluded that "I am not convinced that *occultus* and *lucifugus* are conspecific. Tentatively, *Myotis occultus* is given specific status." (Hoffmeister, 1986:76). However, Valdez et al. (1999a) came to the alternate conclusion based on protein electrophoresis of soft tissues. They examined 20 protein loci and found nine to be polymorphic. They examined variation in these polymorphic loci among nine sample groups totaling 142 bats. These sample groups corresponded to *M. lucifugus carissima* populations in southern Wyoming, *M. occultus* populations in New Mexico, and presumed intergrade populations (based on Findley and Jones [1967]) in southern Colorado (Valdez et al., 1999a). No fixed allelic differences and high genetic similarity were found among these sample groups based on the protein electrophoresis, leading Valdez et al. (1999a) to conclude that the name *occultus* should be retained as a subspecies based primarily on morphological differences.

Current Classification as a Full Species: Molecular analysis of the species question was taken a step further by sequencing 1,478 combined base pairs of the complete cytochrome oxidase II (COII) gene and the partial cytochrome-b gene (mitochondrial DNA) from a small subset of the individuals sampled by Valdez et al. (1999a) in New Mexico, southern Colorado, and Wyoming (Piaggio et al., 2002). Based on a series of complex phylogenetic analyses, Piaggio et al. (2002:391) concluded "Our results suggest that *M. occultus* represents an evolutionarily distinct monophyletic lineage and that it is separated from *M. l. carissima* by sufficient genetic distance to be considered a separate species." The samples from southern Colorado were genetically similar to *M. occultus* from elsewhere and distinct from *M. lucifugus carissima*, despite being morphologically intermediate (Piaggio et al., 2002). As part of a larger dissertation on western species of *Myotis*, Dewey (2006) analyzed a subset of the genetic data as deposited in GenBank from the same eight specimens analyzed by Piaggio et al. (2002). This subset initially involved about 800 base pairs from only the mitochondrial cytochrome b gene, with sequences subject to grouping through parsimony analysis. This smaller genetic data set led her to the conclusion that the samples fell within *M. lucifugus,* but that they included four individuals that formed a well-supported clade (Dewey, 2006). However, these four individuals did not represent geographically distinct populations and were from locations scattered across the recognized distribution of *M. occultus*, ranging from Grant County in southwestern New Mexico to Las Animas County in southeastern Colorado (Dewey, 2006), making interpretation difficult. Additional phylogenetic analysis of the full 1,140–base-pair mitochondrial cytochrome b gene (but including only one sample from New Mexico) supported the divergence of *M. occultus* as a species distinct from *M. lucifugus*, although a much closer relationship was indicated by analysis of the nuclear Rag 2 gene (Stadlemann et al., 2007).

Based on morphological analysis of multiple cranial characters of 268 Arizona myotis from New Mexico and southern Colorado, as well as specimens of *M. lucifugus carissima* from Wyoming, findings of Valdez (2006) supported the specific status of *M. occultus* and suggested that the southern Colorado population was more isolated and smaller in size than New Mexico populations (see also "Foraging and Dietary Analysis" below).

Habitats and Relative Abundance.— Findley et al. (1975) concluded that Arizona myotis were usually found in association with large permanent water sources and that vegetation zones were seemingly unimportant in determining their distribution. Other authors also have noted that roosts are often located near streams, rivers, or lakes in a wide variety of habitat types (for example, Stager, 1943b; Mumford, 1957; Hayward, 1963; Geluso and Studier, 1979; Geluso and Mink, 2009). They are often reported at higher elevation sites (1800–2750 m; Barbour and Davis, 1969, 1970) but are also known from lowland deserts (for example, Geluso and Mink, 2009; Calvert and Neiswenter, 2012) as well as intermediate elevations.

Arizona: This species was the fourth most frequently captured (115 individuals) among 11 species and 1,119 individuals documented in mist nets over water in ponderosa pine forest habitat in northern Arizona, and the third most frequently captured species (109 captures among 554 bats of 15 species) in northern Arizona ponderosa pine-Gambel oak (*Quercus gambelii*) habitat (Morrell et al., 1999). They also ranked third most frequently captured (54 captures among 353 bats of 15 species) in ponderosa pine forests on the Tonto National Forest in central Arizona at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim (Lutch, 1996). They ranked fourth in relative abundance (199 captures among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). A mist-netting survey in five riparian canyons in the Huachuca Mountains in southern Arizona during 1993 and 1994, however, found them to rank last in relative abundance among 13 species (one capture out of 145 individuals; Sidner and Davis, 1994). These bats have been captured in flight among pockets of human-restored cottonwood-willow riparian habitats along the lower Colorado River in southwestern Arizona, vegetation types that have been much reduced due to human influences (Calvert and Neiswenter, 2012).

Colorado and New Mexico: Arizona myotis ranked sixth most abundant among 15 species captured (100 out of 1,996 individuals) at Mesa Verde National Park in southwestern Colorado during 2006 and 2007 (O'Shea et al., 2011a). In an earlier study at Mesa Verde National Park during 1989–1994, they ranked low in relative abundance, with one capture among 189 bats of 11 species (Chung-MacCoubrey and Bogan, 2003). Bogan et al. (1998) did not document any of these bats among 15 species and 1,532 bats captured in the Jemez Mountains in the north-central part of the state. Arizona myotis ranked second in relative abundance (30 bats captured among 130 individuals of six species) netted over water along the middle Rio Grande in the Bosque del Apache National Wildlife Refuge in central New Mexico (Chung-MacCoubrey, 1999). They ranked as lowest in abundance among 16–17 species (one bat out of 855 individuals) captured in mist nets over ponds during 1970 at Nogal Canyon in the San Mateo Mountains, Socorro County, New Mexico, in habitats described as pinyon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974).

These bats were observed both foraging and drinking over the Gallinas River in northern New Mexico (Geluso and Studier, 1979). Although they are typically found in areas near permanent water (Findley et al., 1975), near Las Vegas, New Mexico they showed a much greater urine concentrating ability after feeding in captivity than little brown myotis from the more humid environment of Indiana (Geluso, 1975; Bassett and Wiebers, 1979).

Arizona myotis ranked ninth in relative abundance (a total of 66) among 1,595 bats of 20 species taken over water in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were found in both xeric shrub grassland and evergreen forest habitats (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, Arizona myotis also ranked ninth of 19 species (32 captures among 1,004 individuals) and were taken at a single streamside site at 2,500 meters elevation in pine-spruce-fir forest (Jones and Suttkus, 1972). Geluso and Geluso (2012) reported that this species was the least abundant bat (one capture among 1,390 bats and 11 species) taken over a 34-year period at a pond in coniferous forest at 2,573 meters elevation in the San Mateo Mountains of New Mexico. Somewhat farther south, Jones (2016) documented bats captured during surveys of the Greater Gila region of Catron, Grant, and Sierra Counties of New Mexico; this species ranked low in abundance, ranking twelfth, with three captures among 282 captures of 16–17 species (Jones, 2016; including data from unpublished reports of others). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species with 110 Arizona myotis, ranking fifth in relative abundance (Geluso, 2006, 2017).

Foraging and Dietary Analysis.— Diets of Arizona myotis vary by location, and this is reflected in cranial morphology. Food habits were analyzed from three populations, one from southern Colorado, one from central New Mexico, and one from southern New Mexico; discriminant function analyses of 24 cranial measurements also were conducted for specimens from these three populations (Valdez and Bogan, 2009). Specimens from southern Colorado were least robust in cranial and dental morphology, with thinner jaws, lower coronoid processes, and narrower width of individual molars when compared to bats from central or southern New Mexico. The diets of bats from southern Colorado consisted mainly of smaller, softer bodied insects, primarily hymenopterans (wasps, bees, and ants) and dipterans (midges), consistent with their less robust cranial morphology, whereas bats from central New Mexico ate significantly more hard-bodied beetles and fewer soft-bodied hymenopterans. Diets of individuals from southern New Mexico were not collected following the same procedures as in the other two populations, but composition was similar to the diet in central New Mexico, with coleopterans predominant and hymenopterans low, but with greater representation of lepidopterans (Valdez and Bogan, 2009). The relationship between regional dietary differences and cranial robustness was speculated to be a reflection of the length of the growing season, which may have impacted abundances of different types of available prey (Valdez, 2006; Valdez and Bogan, 2009). Overall the diet included seven orders of insects as well as minor numbers of arachnids, with insect orders identified to 18 families (Valdez and Bogan, 2009). Eight orders of insects were reported in Arizona myotis diets from ponderosa pine forests in northern Arizona at 2,600 meters elevation, with lepidopterans at the highest frequency of occurrence followed by coleopterans and dipterans (Warner, 1985).

Roosting Habits.— Winter Roosts: Little is known about winter hibernation sites of Arizona myotis, although it is suspected that hibernacula are not far from summer sites (for example, Findley et al., 1975; Geluso, 2007). Unpublished records exist for small numbers of individuals hibernating in a mine in southeastern California and in a mine in Sonora, Mexico (Arizona Game and Fish Department, 2011). Mist netting of bats during winter months in central and southern New Mexico yielded only one individual (in late March), although intermittent activity of 11 other species was detected from November to March through captures of 401 individuals (Geluso, 2007). Cockrum et al. (1996) speculated that Arizona myotis from lower elevations along the Colorado River in Mohave County, Arizona, may move upstream to hibernacula at higher elevations. It also has been speculated that they may overwinter by hibernating in inconspicuous rock crevices at higher elevations (O'Shea et al., 2011a) similar to overwintering habits of big brown bats on the eastern slope of the Rocky Mountains (Neubaum et al., 2006) and Alberta, Canada (Klüg-Baerwald et al., 2017), and postulated for western bats in general by Twente (1960).

Warm Season Roosts: Live trees, snags, and buildings are used as warm season roosts by this species in Arizona. In northern Arizona, Rabe et al. (1998a) radio tracked 22 adult females and found 21 of these bats roosting in ponderosa pine snags and one Douglas fir snag, with one roosting in the attic of a cabin. Thirty adults were radio tagged on the Tonto National Forest of central Arizona and tracked to 21 roosts (Lutch, 1996). Fourteen roosts were located in trees, with 11 in ponderosa pine snags, two in live ponderosa pines, and one in a living Arizona white oak (*Quercus arizonica*); four roosts were in buildings, one was behind a board on a fencepost (used once by a solitary non-reproductive female), and one in a utility pole. The trees used for roosts averaged 17 meters in height (range 6.2 to 30 meters) and were taller than the average height of trees in the surrounding stand, with heights of roost openings averaging 9.8 meters (range five to 16.5 meters) and openings variable in aspect (Lutch, 1996). Two roosts were discovered by tracking a male, who roosted alone under loose bark of a ponderosa pine and in a crack in the trunk of an alligator juniper (*Juniperus deppeana*). Maternity colony size in the attic of a house used by several tagged bats ranged 20–51 individuals, and over 100 used one barn, with 35 counted in a second barn; 13 bats roosted in the utility pole (Lutch, 1996). Mean colony size at roosts (including trees) used by ten tagged individuals was 86 ± 29.6 (SE) bats, but one colony in a ponderosa pine snag numbered 325 bats. Some roosts were not used in the following year, and many roosts were not occupied consistently in a single season. Ten tagged bats switched roosts every 1.9 ± 0.27 (SE) days (Lutch, 1996). Arizona myotis (n = 20 females) radio tracked in east-central Arizona ponderosa pine forest roosted in 22 snags (20 in ponderosa pine, two in Douglas fir), with mean colony sizes of 152 bats observed in exit counts (range up to 305; Saunders, 2015).

Roost use by individual bats can sometimes be quite variable. One of five reproductive females radio tracked at Mesa Verde National Park in southwestern Colorado used multiple roosts during a summer, including a rock crevice, a ponderosa pine snag, and a building in the nearby, lower elevation, irrigated Mancos Valley. The remaining four bats roosted only in buildings in the valley and were located an average of 6.8 ± 5.3 (SD) kilometers from points of capture (O'Shea et al., 2011a). Five reproductive females captured while foraging at the Bosque Del Apache National Wildlife Refuge were radio tagged, with three maternity colony sites and four solitary bat roosts discovered (Chung-MacCoubrey, 1999). Two colonies, one composed of over 500 bats and one of about 90 bats, roosted under sloughing bark of dead cottonwood trees (*Populus fremontii*) killed by fire, as did four solitary individuals in smaller trees. The roost of a third colony was in a church 13 kilometers north of the refuge and housed over 1,800 individuals of both Arizona myotis and Yuma myotis combined (Chung-MacCoubrey, 1999).

Colonies of Arizona myotis with numbers as high as the thousands are well-known to roost in human-made structures. A maternity colony of about 800 was reported roosting in multiple small, vertical crevices under a wooden bridge in the Lower Colorado River Valley of southern California during spring and summer months of 1939 (Stager, 1943b). The bridge also was used by Brazilian free-tailed bats and Yuma myotis (*M. yumanensis*), species commonly found to share roosts. A lone male also was found in a 'shallow pocket' in the rock wall of an abandoned mine in the Riverside Mountains in the same region (Stager, 1943b). In New Mexico, a colony of unreported size roosted in a building at Bosque Del Apache National Wildlife Refuge (Mumford, 1957), and a maternity colony of several hundred Arizona myotis was reported from an attic of a seminary in San Miguel County that was the subject of several physiological ecology studies during 1966–1971 (for example, Studier and O'Farrell, 1972; O'Farrell and Studier, 1973; Geluso and Studier, 1979). This colony sharply increased in size during 1970, peaking at about 15,000 individuals (O'Farrell and Studier, 1975). An attic of a home in the same region was reported to house a maternity colony estimated at 4,400 at peak summer size (O'Farrell and Studier, 1975). Hundreds of individuals were found roosting in diurnal colonies in narrow cracks and crevices under nine highway bridges over the Rio Grande in southern New Mexico during 2004–2006, including two maternity colonies in bridges constructed of timbers; roosting sites were at least 1.1 meters above ground (Geluso and Mink, 2009). A maternity colony of unreported size was found in the attic of an abandoned home in the Verde Valley of Arizona in 1960 and 1961 (Hayward, 1963). In human-made structures, Arizona myotis colonies will often occur with colonies of other species, including Yuma myotis, big brown bats, and fringed myotis (Studier, 1968; Geluso and Mink, 2009).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Surprisingly little has been published on litter size in the Arizona myotis, although the presumption that only one young is born each year is likely valid. Single embryos were found in an adult female from Bosque Del Apache National Wildlife Refuge, a female from Santa Rosa, and an unspecified number of females from near Montezuma, all in New Mexico (Bailey, 1931; Mumford, 1957; Studier and O'Farrell, 1972; O'Farrell and Studier, 1973; Studier et al., 1973).

Natality has been investigated in this species at several locations, but proportions of females breeding may be biased high in samples taken at maternity roosts. In New Mexico, all of 240 females examined at a maternity roost in Las Vegas were reproductive in 1969 (O'Farrell and Studier, 1975; it is unclear if reproductive bats were intentionally selected), "about 90%" were pregnant the following year (O'Farrell and Studier, 1975:370; number examined not stated), and 43 of 47 (91%) captured both at roosts and over water in the Mogollon Mountains (including adjacent Arizona) during June and July in 1959–1962 were reproductive (C. Jones, 1964). In southern Colorado during 1968, 67 of 70 (96%) adult (greater than one year old) females examined at maternity roosts at three locations were reproductive (Davis and Barbour, 1970). However, females do not all breed in their first year of life. Only one of 35 one-year-old females examined at four locations (including maternity colonies) in Colorado and New Mexico in summer 1968 were reproductive, compared to 97 of 109 (89%) older adults (Davis and Barbour, 1970).

In northern Arizona, 12 of 38 (32%) females captured over water in ponderosa pine forest during 1993–1995 were reproductive, whereas 39 of 51 (76%) females captured over water in pine-oak forest during summers 1994–1995 were reproductive (Morrell et al., 1999). In New Mexico, 12 of 16 (75%) females captured over water at Bosque del Apache National Wildlife Refuge in 1997 were reproductive (Chung-MacCoubrey, 1999), and 19 of 28 (68%) examined at a night roost at Eagle Nest in 1968 were reproductive (Davis and Barbour, 1970). At Mesa Verde National Park in southwestern Colorado 18 of 22 females (82%) captured over water during 2006 and 2007 were reproductive, with no differences between years despite a prolonged drought and reduced insect abundance in 2006; it was suggested that these bats maintained higher reproductive rates because of foraging access to the irrigated Mancos Valley where roosts were located (O'Shea et al., 2011a). The proportion reproductive for the cumulative total females taken away from maternity roosts over all U.S. locations and years was 65% (100 of 155 bats).

Survival: Diamond et al. (2015) investigated population dynamics of Arizona myotis roosting in wooden bat boxes placed on six ponderosa pines (four boxes per tree) within each of 24 one-hectare study plots in northern Arizona during 2005–2012. Bands were placed on 227 individuals across all years, and Cormack-Jolly-Seber recapture models for open populations were applied to estimate abundance, apparent survival, and indirect recruitment based on three to five capture attempts at roosts each summer. Most (165) of the banded bats were never recaptured. Apparent survival estimates over the course of the study were 0.64 ± 0.17 (SD) for females and 0.45 ± 0.32 for males (Diamond et al., 2015) and varied by sex and year. These estimates appear unsustainable (see review in O'Shea et al., 2011c) but possibly may include permanent emigration, banding-caused mortality (Hitchcock, 1965; O'Shea et al., 2004), or other unknown effects. Females were recaptured more often than males, indicating greater roost fidelity, with capture probabilities of 0.63 ± 0.18 (SD). Estimated population size (all inferences presumably for the 24 one-hectare plots sampled) varied each year from 41 to 68 females, and 26 to 143 males. Results suggested that overall population growth rates were flat and not increasing (Diamond et al., 2015).

Mortality Factors: Neonatal mortality in Arizona myotis is low, estimated at about 2% for a colony studied in an attic near Las Vegas, New Mexico (O'Farrell and Studier, 1973). Ectoparasites have been well documented (Valdez et al., 2009), helminths reported (Cain and Studier, 1974), and coronaviruses have been detected (Dominguez et al., 2007), but no mortality from these agents has been described. These bats are undoubtedly susceptible to rabies virus infection, but the literature on rabies in bats does not distinguish *M. occultus* from *M. lucifugus*. No mortality due to exposure to environmental contaminants has been described, although monitoring for metals and radiation is planned for bats sampled at a uranium mine site in Arizona (Hinck et al., 2014).

Population Trend: Other than occasional estimates of colony sizes and results of Diamond et al. (2015) given above, we found no information on population size and trend for the Arizona myotis (see also "Survival" above for an analysis at one study site). Pierson and Rainey (1998d) noted that the bridge housing the maternity colony reported by Stager (1943b) as subsequently demolished and replaced; the fate of that colony was unknown, and the species had not been documented in California since a single record in 1969. However, 17 individuals (including reproductive females) were captured on the Arizona side of the lower Colorado River on the 'Ahakhav Tribal Preserve and the Cibola Valley Conservation Area about 0.5 kilometers from the California border in 2007 and 2010 (Calvert and Neiswenter, 2012).

MANAGEMENT PRACTICES AND CONCERNS.— In studies of several species of bats (including the Arizona myotis) roosting under loose bark or in lightning-caused cracks of snags in northern Arizona, Rabe et al. (1998a) recommended measures to help recruit snags with loose bark as bat roosts. They suggested that forest management should retain large trees that die in place, should thin stands of small trees to allow faster development of larger trees, and should kill live large trees in areas of low snag density to hasten roost development. Prescribed fire with protection of existing snags also may help promote development of future snags (Rabe et al., 1998a).

Arizona myotis will use artificial roosts constructed to mimic exfoliating bark on snags in ponderosa pine forests in northern Arizona, where they also will occupy wooden bat boxes (Mering and Chambers, 2012; Diamond et al., 2015). The species has been captured in flight within experimentally restored cottonwood-willow riparian habitats along the lower Colorado River (Calvert and Neiswenter, 2012).

Considering the close taxonomic relationship between Arizona myotis and little brown myotis, the latter of which is among the most susceptible to white-nose syndrome (Frick et al., 2010a), monitoring populations of Arizona myotis may help with early detection of disease arrival in southwestern regions of the U.S.

Myotis thysanodes — Fringed myotis (Family Vespertilionidae)

CONSERVATION STATUS.— **National and International Designations:** U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species (*M. thysanodes, M. thysanodes vespertinus*). Bureau of Land Management (2009a,b, 2010a,b,c, 2011b, 2015a,b): Sensitive Species (California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Wyoming state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Species Rounded Global Status G4, Apparently Secure; subspecies *M. thysanodes pahasapensis* and *M. thysanodes vespertinus* Rounded Global Status T2, Imperiled.

State Designations: California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. Colorado Parks and Wildlife (2015b): Species of Greatest Conservation Need, Tier I. Idaho Department of Fish and Game (2005): Species of Greatest Conservation Need (not included in Idaho Department of Fish and Game, 2015). Montana Fish, Wildlife, and Parks (2015a,b): Species of Concern, Species of Greatest Conservation Need S3. Nebraska Game and Parks Commission (2011): At-Risk Species Tier I (as *M. t. pahasapensis*). Nevada Department of Wildlife (2013): Protected Mammal, Species of Conservation Priority. Nevada Department of Conservation and Natural Resources (2015a): S2 Imperiled. Oregon Department of Fish and Wildlife (2005, 2008): Sensitive Species, Vulnerable. South Dakota Game, Fish, and Parks (2014): Species of Greatest Conservation Need (as *M. t. pahasapensis*). Texas Parks and Wildlife (2012): Species of Greatest Conservation Need, Vulnerable. Utah Division of Wildlife Resources (2015; Sutter et al., 2005): Species of Greatest Conservation Need. Washington Department of Fish and Wildlife (2015a): Species of Concern. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier II.

FIGURE 31. Fringed myotis, *Myotis thysanodes* (photo by J. Scott Altenbach).

DESCRIPTION.— The fringed myotis (Fig. 31) is a medium to large sized myotis with large ears that extend about three to five millimeters beyond the snout when laid forward (Miller, 1897). Forearm lengths range 39–47 millimeters, and ear lengths 12–22 millimeters (for example, Barbour and Davis, 1969; O'Farrell and Studier, 1980; Hoffmeister, 1986). Body mass ranges six to nine grams (Armstrong et al., 2011; Ammerman et al., 2012a), with individuals recorded as high as 11.7 g during autumn fat deposition (Ewing et al., 1970). The short, dense fringe of hair on the distal edge of the uropatagium is distinctive, but a much less pronounced fringe can sometimes be discerned on the trailing edge of the tail membrane of the long-eared myotis (sometimes best seen with magnification). The long-eared myotis also is smaller than the fringed myotis and has longer and darker (blackish) ears. The two species are reported to be difficult to distinguish in hand in western South Dakota and eastern Wyoming (see personal communications in Dewey, 2006).

Distribution and Systematics.— The fringed myotis is found in the western United States, western Canada, and Mexico (Fig. 32). In the United States, the distribution includes all or parts of the following states: Arizona, California, Colorado, Idaho, Nebraska, Nevada, New Mexico, Oregon, South Dakota, Texas, Utah, Washington, and Wyoming (O'Farrell and Studier, 1980).

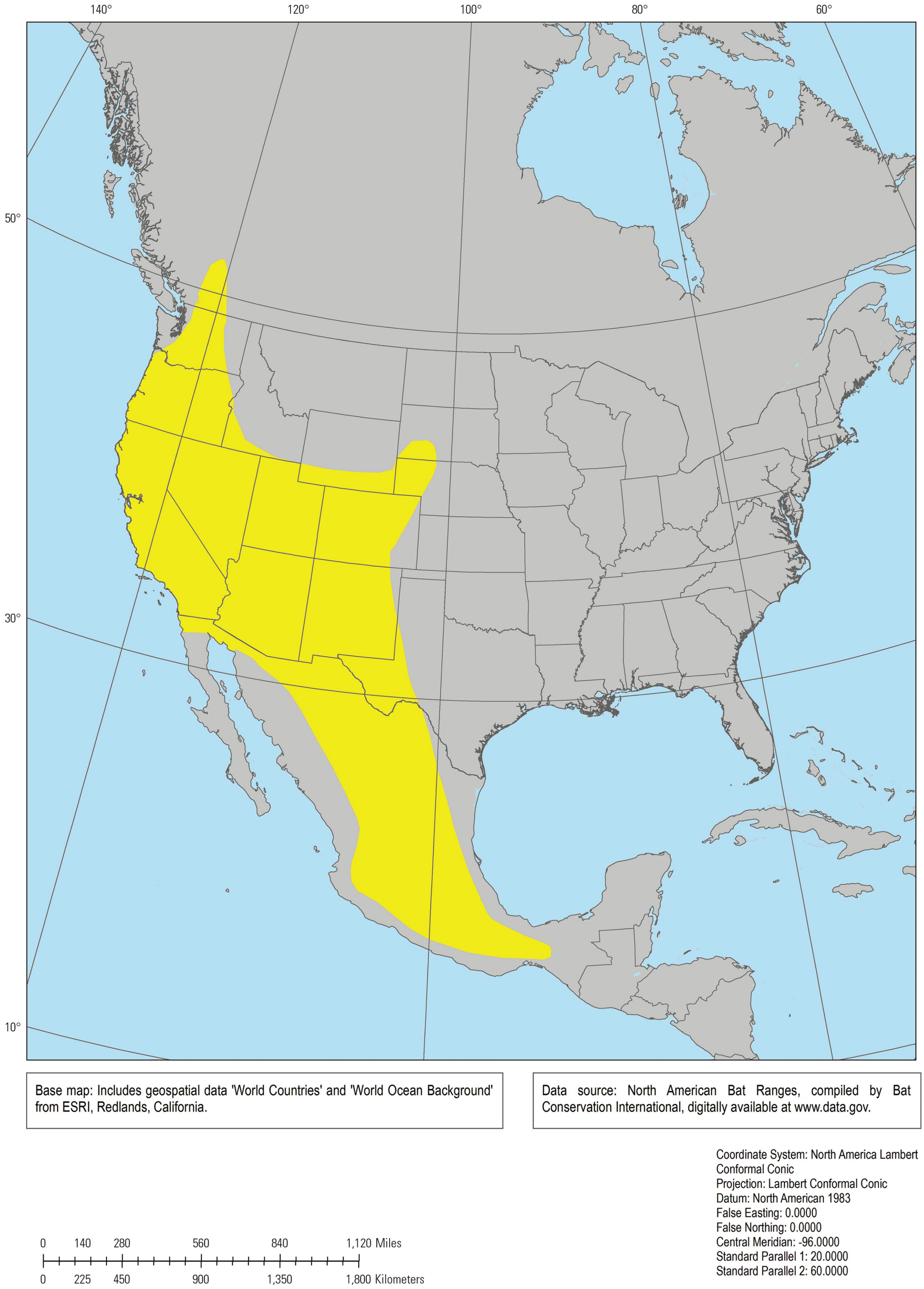
There have been no major changes to the nomenclature of this species since the original description by Miller (1897). Four subspecies are recognized (Miller, 1897; Miller and Allen, 1928; Jones and Genoways, 1967; Manning and Jones, 1988). *M. thysanodes thysanodes* occurs in the western United States in suitable habitat from western Texas through New Mexico, Arizona, Utah, Colorado, southern Wyoming, Idaho, Nevada, California, Oregon, and Washington; *M. thysanodes aztecus* is found in south central Mexico (Oaxaca); *M. thysanodes pahasapensis* is found in southwestern South Dakota, northwestern Nebraska, and eastern Wyoming; and *M. thysanodes vespertinus* is reported to occur in southwestern Washington, western Oregon, and northwestern California. The validity of these subspecies designations has not been investigated with modern genetic approaches. Other English common names include fringed bat and fringe-tailed myotis. The specific epithet stems from the Greek *thysanos*, meaning "fringe" or "tassel", and *odes*, meaning "resemblance".

Analyses and discussion of molecular genetic relationships of the fringed myotis to other species of myotis and possible genetic-based groupings within *M. thysanodes* have been provided by recent authors, including Dewey (2006), Stadlemann et al. (2007), Carstens and Dewey (2010), and Vonhof et al. (2015). These studies suggest close evolutionary relationships of fringed myotis with the long-eared myotis, Keen's myotis, and one subspecies of the little brown myotis. Relationships among some of these species based on morphology, allozyme variation, and other traits also have been hypothesized (for example, Reduker et al., 1983).

Habitats and Relative Abundance.— Early mammalogists referred to habitat used by fringed myotis as the Upper Sonoran or Transition life zones, from about 1,200 meters up to about 2,500 meters in elevation (Grinnell, 1918; Bailey, 1931). These ranges in habitat remain valid as generalizations based on additional studies, but elevations as high as 2,850 meters in spruce forest and as low as sea level have been since recorded (for example, Orr, 1956; Davis and Barbour, 1970; Hayes, 2011). Relative abundances of this species in bat community surveys vary among regions and habitats range-wide. This species often ranks from low to intermediate in relative abundance in these surveys.

Pacific Northwest and Northern Rocky Mountains: Fringed myotis were low in relative abundance in most surveys in the Pacific Northwest and northern Rockies. In northeastern Oregon, they were found to be uncommon or difficult to collect across a variety of habitat types (Whitaker et al., 1981). Captures of night-roosting bats at five bridges in western hemlock forest in the Willamette National Forest of Oregon included eight species and 412 individuals, but no bats of this species (Perlmeter, 1996). They were very rarely captured in forests of multiple types in northern Idaho (two bats captured for fecal analysis among 187 individuals of eight species taken; Lacki et al., 2007). These bats ranked third in relative abundance (137 captures of 1,057 individuals of 11 species), however, among bats captured over water in the predominantly ponderosa pine forests of the eastern Cascade Mountains of south-central Washington (Baker and Lacki, 2004). Netting results at 52 sites sampled in predominantly ponderosa pine forests of the eastern Cascades in both Washington and Oregon suggested they were locally common but rare across all study locations (Lacki and Baker, 2007).

Fringed myotis were not captured among 231 individuals of nine species of bats netted over water in the Pryor Mountains of south-central Montana (Worthington, 1991). This species ranked eighth in relative abundance (six individuals) among 12 species and 958 bats captured over water



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 32. Approximate distribution of the fringed myotis, *Myotis thysanodes*.

in the semi-arid Okanagan Valley of southern British Columbia (Woodsworth, 1981). They ranked eighth in relative abundance (two captures) in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water (Fenton et al., 1980).

California and Nevada: Fringed myotis were lowest in relative abundance (three bats captured among 403 bats of 10 species) in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests (Duff and Morrell, 2007). A survey based on mist netting over water in old growth redwood forest in a Coastal Range locality of northern California failed to document this species among 142 bats of seven species captured (Zielinski and Gellman, 1999). They were rarely taken in mist nets set over water in montane hardwood/conifer habitats along the upper Sacramento River in northern California (Siskiyou and Shasta counties), ranking tenth with just five individuals captured among 1,398 individuals of 15 species documented during 1991–1995 (Pierson et al., 1996b). They were rarely taken at night roosts at bridges in the study area, where just three were captured in comparison with 2,132 individuals of nine other species (ranking eighth in relative abundance; Pierson et al., 1996b). Similarly, fringed myotis ranked thirteenth of 17 species (five individuals among 390 bats) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999, where they were considered rare (Pierson et al., 2001). In contrast, results of netting both over water and within forests in Yosemite National Park in the California Sierra Nevada Range, concentrating on groves of giant sequoia (*Sequoiadendron giganteum*) trees, suggested that these bats were more common than six other species, ranking fourth among ten species with 44 captures among 284 individuals in total (Pierson et al., 2006). Higher relative abundance of fringed myotis in the Yosemite study may in part have been due to proximity to subsequently discovered roosts, particularly in one grove of sequoias where they were the most frequently encountered species by both mist net and acoustic sampling (Pierson et al., 2006).

Fringed myotis have not been commonly reported in surveys in Nevada. They were not documented in mist-netting surveys encompassing five habitat zones (ranging from Mojave mixed desert scrub to alpine) in the White and Inyo Mountains of California and Nevada, although about 2,000 bats of 13 species were captured (Szewczak et al., 1998). They also were not documented in mist-netting surveys over water in west-central Nevada in habitats categorized as desert shrub, piñon-juniper woodland, or deciduous riparian trees, where a total of 299 bats of 11 other species were captured (Kuenzi et al., 1999). Mist netting over water and captures at abandoned mines and tunnels in six habitat zones of eastern Nevada documented 578 individuals in twelve species, but no fringed myotis (Ports and Bradley, 1996). However, Hall (2000) documented the species in Great Basin and Mojave Desert habitats on the Nevada Test Site in south-central Nevada, ranking tenth with 28 captures among more than 2,000 individuals of 13 species sampled over water.

Southwestern U.S.: ***Arizona*:** Fringed myotis ranked fourth in abundance among 15 species (122 bats captured out of 1,673 individuals) netted over water during 1993–1995 in ponderosa pine and ponderosa pine-Gambel oak woodlands at 2,200 to 2,600 meters elevation on the Coconino Plateau of northern Arizona (Morrell et al., 1999). This species also ranked fourth in abundance among 17 species of bats (142 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). They ranked sixth in relative abundance (135 taken among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). However, they ranked lowest in relative abundance (one bat among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters along the

East Verde River below the Mogollon Rim on the Tonto National Forest in central Arizona (Lutch, 1996). In Mohave County, western Arizona, where elevations ranged from 60 to 2,566 meters, they ranked third in relative abundance, with 432 captures among 3,458 individuals of 18 species netted over water; most capture sites appear to have been above about 1,280 meters with most suitable habitat referred to as oak and pine forest of the upper Sonoran and Transition life zones (Cockrum et al., 1996). They were reported as commonly netted over water among oaks in the Chiricahua Mountains of southeastern Arizona (Barbour and Davis, 1969). A mist-netting survey in five riparian canyons in the Huachuca Mountains in southern Arizona during 1993 and 1994 found this species to rank sixth in relative abundance among the 13 species documented (seven captures out of 145 individuals; Sidner and Davis, 1994).

***New Mexico*:** In the Gallinas Mountains of New Mexico, this species is commonly associated with piñon-juniper woodlands (Chung-MacCoubrey, 2005), where although they were the least abundant myotis, they ranked fifth among all species in relative abundance (68 captures among 1,222 bats of 10–11 species). In ponderosa pine forests of New Mexico's San Mateo Mountains, they ranked third in relative abundance, with 58 captures among 447 bats of seven to eight species, and they were captured at higher rates than in the piñon-juniper woodlands of the Gallinas Mountains (Chung-MacCoubrey, 2005). Fringed myotis were low in abundance, ranking eleventh among 16–17 species (10 bats among 855 individuals) captured in mist nets over ponds during 1970 at Nogal Canyon in the San Mateo Mountains, Socorro County, New Mexico, where habitats were described as pinyon-juniper woodland, pine-oak woodland, and mixed-conifer forest (Black, 1974). Somewhat farther south, Jones (2016) documented bats captured during surveys of various habitats in the Greater Gila region of Catron, Grant, and Sierra Counties of New Mexico; they ranked fifth in relative abundance and were mostly captured in ponderosa pine forest, with 20 captures among 282 individuals of 16–17 species (Jones, 2016; including data from unpublished reports of others).

Fringed myotis were of low to intermediate abundance (a total of 84), ranking eighth among 1,595 bats of 20 species captured in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were most common in evergreen forest above 2,134 meters (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, these bats ranked seventh of 19 species (33 captures among 1,004 individuals) and were taken at all three sites; habitat at capture sites ranged from riparian hardwoods at 1,465 meters to pine-spruce-fir forest at 2,620 meters elevation (Jones and Suttkus, 1972). In the Jemez Mountains of New Mexico, they also were low to intermediate in relative abundance (69 captures among 1,532 captures of 15 species, ranking seventh) and were netted over water at elevations ranging from 1,753 to 2,774 meters (Bogan et al., 1998). Echolocation activity of fringed myotis was commonly detected in riparian, conifer, piñon-juniper, and previously (20 years prior) intensely burned ponderosa pine habitat in the Jemez Mountains (Ellison et al., 2005). Fringed myotis ranked third in abundance (126 among 1,390 bats and 11 species) during 19 years of netting spanning 1971–2005, in ponderosa pine/mixed pine forests at elevation 2,573 meters in New Mexico (Geluso and Geluso, 2012). They ranked fourth in relative abundance (15 among 302 bats of 10–11 species) netted over water in mostly ponderosa pine habitat at 2,600 to 2,885 meters on Mount Taylor in northern New Mexico (Geluso, 2008). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species, with 80 fringed myotis ranking ninth in relative abundance (Geluso, 2006, 2017).

***Texas*:** In Big Bend National Park in Texas, fringed myotis were moderately abundant (400 captured among 4,807 bats of 18 species at 32 localities, ranking sixth) throughout the park (across four vegetation zones, described as river floodplain, shrub desert, woodland, and moist Chisos woodland) during 1967–1971, but they were most frequently captured in the lower-elevation habitats (Easterla, 1973). However, they were rarely captured (two captures among 1,978 bats of 17 species) in a subsequent study during 1996–1998 that emphasized surveys in lowland habitat at the park (Higginbotham and Ammerman, 2002). Fringed myotis ranked eleventh among 14 species (two out of 542 individuals) captured in mist nets at 108 locations over water in northern Chihuahuan desert habitats at Big Bend Ranch State Park in the Trans-Pecos region of Texas; the two bats were captured over pools in sparsely vegetated areas within canyons (Yancey, 1997).

Central Rocky Mountains and Western Great Plains: *Colorado and Utah*: The fringed myotis is moderately abundant in Colorado. They have been found in ponderosa pine and Douglas fir forests along the Colorado Front Range in Boulder County, where they ranked fourth in relative abundance in one study, with 157 captured among 1,398 bats of 10 species documented during 1996–2000 (Adams et al., 2003), but ranked eighth out of nine species in a second survey in the mountains to the north in Larimer County, with 10 captured among 634 individuals (O'Shea et al., 2011b). This species was rarely reported in the urban or urbanizing corridor east of the Colorado Front Range (O'Shea et al., 2011b). They ranked tenth among 15 species with 41 bats out of 1,996 individuals captured at Mesa Verde National Park in southwestern Colorado during 2006–2007, but fifth among 11 species (nine bats out of 189 individuals) during an earlier study that concentrated netting at small, isolated pools (Chung-MacCoubrey and Bogan, 2003; O'Shea et al., 2011a). They were the least abundant species (three captures among 546 bats of 11 species) captured over ponds during surveys in piñon-juniper woodland at about 2,100 meters elevation in the Uintah Basin of Moffat County in northwestern Colorado during 1979–1981 (Freeman, 1984). In western Colorado, this species ranked eighth in relative abundance of 16 species (22 among 899 bats) captured at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Fringed myotis ranked eleventh in abundance (31 captures among 1,377 bats of 15 species) in surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

At Arch Canyon on the Colorado Plateau in southeastern Utah, these were the least abundant species, with one bat captured among 295 bats of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016). In the Henry Mountains of southeastern Utah, they ranked eighth in relative abundance of 15 species (34 captures among 572 individuals), where they were taken between 1,295 and 2,713 meters (Mollhagen and Bogan, 1997).

***Wyoming and South Dakota*:** During 2012, fringed myotis ranked tenth of 12 species in relative abundance (four captured among about 370 individuals) documented by mist netting in lower elevation basin and foothills habitat in the south-central part of Wyoming (Abernethy et al., 2013). None were taken in surveys in lodgepole pine and spruce-fir forests of the Medicine Bow National Forest in southern Wyoming (where 246 bats of six species were documented; Gruver, 2002), nor during late summer-early autumn netting in primarily lodgepole pine, Engelmann spruce, subalpine fir, and Rocky Mountain juniper forests on the northern range of Yellowstone National Park, northwestern Wyoming (where 112 bats of seven species were captured; Johnson et al., 2017).

Fringed myotis are moderately abundant in parts of South Dakota, were they were the third most abundant species of bat (187 captures among 1,197 individuals of seven species) and the second most abundant species of *Myotis* captured in predominantly ponderosa pine forest in the southern Black Hills (Cryan et al., 2000). They were the fourth most common species in sampling at Badlands National Park in South Dakota (29 individuals among 405 bats of nine species; Bogan et al., 1996).

Elevational Differences in Habitats among Sex and Age Classes: In topographically diverse areas, there are elevational effects on distribution of reproductive female fringed myotis. It has been long known by naturalists that whereas males may use higher elevations, females of several species of western bats tend to use lower elevations to form maternity colonies (for example, Howell, 1920a). Warmer temperatures at lower elevations are more favorable for rapid growth and development of young, whereas cooler temperatures at higher elevations can allow deeper daily torpor for males and non-reproductive females (for example, Cryan et al., 2000; Bogan and Mollhagen, 2016; see review in Weller et al., 2009). Males and non-reproductive females tend to be found in higher proportions at higher elevations. Elevational differences in distribution of the sexes for fringed myotis were reported for the Black Hills of South Dakota, where captures at upper elevations were disproportionately males and non-reproductive females with reproductive females more often captured at lower elevations (Cryan et al., 2000). In Badlands National Park, South Dakota, 24 of 29 (83%) captured at multiple sites were males (Bogan et al., 1996). Cockrum et al. (1996) reported that these bats separate into male colonies and female colonies in summer in Mohave County, Arizona, with male colonies at higher elevations.

In the Cibola National Forest of New Mexico, Chung MacCoubrey (2005) found a significant effect of elevation on probability of capturing reproductive female fringed myotis compared to non-reproductive females and males, with a higher proportion of reproductive females in summer in the lower elevation (2,133 to 2,573 meters) piñon-juniper dominated Gallinas Mountains than in the higher elevation (2,347 to 2,682 meters) ponderosa-pine dominated San Mateo Mountains. Geluso and Geluso (2012) reported that 121 of 126 individuals captured during 19 years of netting in ponderosa pine/mixed pine forests at elevation 2,573 meters in the San Mateo Mountains of New Mexico were adult males. Hayes and Adams (2014) compiled 729 capture and occurrence records for this species in Colorado, mapped the records, and analyzed a subset of these data (546 records) for patterns by sex, reproductive status, and elevation. Mean elevations of reproductive females and juveniles were similar at 1,862 and 1,843 meters with similar confidence intervals; these confidence intervals did not overlap those for the higher mean elevations of records for non-reproductive females (1,976 meters) and males (2,003 meters non-reproductive males, 1,941 meters reproductive males; Hayes and Adams, 2014). (Records were available from 23 of 64 counties in Colorado that encompassed a variety of habitats, although 408 of the 729 records were based on intensive sampling in Boulder County [Hayes, 2011]).

Foraging and Dietary Analysis.— The foraging flight of fringed myotis has been described as “fluttering and soaring” (Dalquest and Ramage, 1946:60). Echolocation detectors tethered to helium balloons demonstrated foraging activity at canopy height (detectors placed at 67 meters within canopies ranging to 82 meters) in groves of giant sequoias in Yosemite National Park, California (Pierson et al., 2006).

Results of dietary analysis seem to vary by study area. Fringed myotis were classified as possible beetle strategists and between-, within-, and below-canopy foragers in dietary analysis of bats sampled in the San Mateo Mountains of New Mexico (Black, 1974). Beetles were also the highest in frequency of occurrence in fecal samples from northern Arizona ponderosa pine forests, followed by moths and dipterans, but they also fed opportunistically on swarms of homopterans (Warner, 1985). In riparian areas in the Oregon Coast Range, this species had a varied diet, eating primarily spiders, lepidopterans, homopterans, and coleopterans in descending order by proportional volume, but also consuming insects in a variety of other groups including dipterans, hemipterans, neuropterans, and orthopterans (Ober and Hayes, 2008). In northeastern Oregon, the diet consisted primarily of lepidopterans and to a lesser extent homopterans and other groups (Whitaker et al., 1981). Similarly, dietary analysis of stomach contents of individuals from northwestern Colorado indicated that lepidopterans were the major dietary component, followed by trichopterans and coleopterans in descending order of proportional frequency, with other groups of insects each constituting less than 10% (Armstrong et al., 1994).

Fringed myotis were among the species sampled by Adams et al. (2003) that seemed to prefer drinking at watering places with higher concentrations of calcium and other minerals; these mineral-rich drinking sites perhaps providing a supplement to dietary intake that would be most critical to reproductive females and weaned volant juveniles.

Roosting Habits.— Early literature suggests that these bats primarily roost in colonies in caves and buildings (for example, Miller and Allen, 1928; Bailey, 1931). More recent research indicates that during warmer months fringed myotis also roost in trees and snags or rock outcrops and cliff faces, with the seeming preference for roosts in rock substrates versus trees varying from study to study, perhaps depending on roost availability.

Winter Roosts: In Washington and Oregon, these bats were infrequently encountered in hibernation during searches of 650 caves or mines during winters 1982–1989, with only two found (one at each of two mines; Perkins et al., 1990). Two hibernating females were reported from an abandoned mine in Mohave County, Arizona, with two hibernating males found in a second mine at 2,134 meters elevation (Cockrum et al., 1996). Although this bat was often captured in mist nets over water in Mohave County during non-winter months, no captures in mist nets were recorded during the months of December through April (Cockrum et al., 1996). Two fringed myotis were found hibernating in an abandoned copper mine in southern Colorado (Ellinwood, 1978). At Jewel Cave in the Black Hills of South Dakota, they roosted singly high on walls in a large chamber during winter (Martin and Hawks, 1972), with only up to 10 positively identified during winter counts (Choate and Anderson, 1997).

Mist netting of bats during winter months in central and southern New Mexico yielded only one fringed myotis (in November), although intermittent activity of 11 other species was detected from November to March by captures of 401 individuals (Geluso, 2007). Given the use of rock crevices as roosts during summer and the lack of observations of large numbers of hibernating individuals observed in caves and mines during winter, it is possible that this species may hibernate in inconspicuous rock crevices and fissures as reported for big brown bats in Colorado (Neubaum et al., 2006) and Alberta, Canada (Klüg-Baerwald et al., 2017), and as was postulated by Twente (1960) for some bats in Utah.

Warm Season Roosts in Trees and Rock Substrates: Studies of warm-season roosting habits of fringed myotis based on radio tracking have been conducted in several regions, including the Pacific Northwest, the southwestern states, the central Rocky Mountain states, and western South Dakota. Lacki and Baker (2007) tracked 25 females in xeric habitats of eastern Oregon and Washington. Females often roosted solitarily or with a single pup. Ninety-three per cent of 118 roosts were in rock crevices and the remainder in snags and downed logs of ponderosa pine trees. Pregnant females tended to choose horizontal rock crevices, whereas lactating females tended to use vertically oriented crevices. Bats used the same roost every 1.8 days on average (range one to 16), with alternate roosts usually within one kilometer of previous roosts. Snags used as roosts were larger and taller than surrounding trees. Although rocks were used as roosts far more frequently, snags held the largest groups (up to 118 bats) counted at emergence (Lacki and Baker, 2007).

In Douglas fir forest in northwestern California, nine radio-tagged fringed myotis of different sex and age classes were radio tracked to 52 day roosts, all located in 23 snags (Weller and Zabel, 2001). Average size of groups emerging from 17 roosts on multiple nights was 31 ± 5 (SE) bats (range one to 88); bats switched roosts after 1.7 consecutive days, with roosts used consecutively ranging from seven to 641 meters apart (Weller and Zabel, 2001). Snags used as roosts all were in early to medium stages of decay, with 20 in Douglas fir snags, one in a ponderosa pine snag, and one in a sugar pine (*Pinus lambertiana*) snag. Snags used as roosts were taller and had greater girth than snags at random sites and were taller relative to canopy height (Weller and Zabel, 2001). In

0.1–hectare plots of forest stands with roosts, characteristics that contributed most to the likelihood that a roost would be used included number of other snags greater than 30 centimeters in diameter, openness of canopy compared to randomly selected 0.1–hectare sites, and in some models distances to stream channels (Weller and Zabel, 2001). In Yosemite National Park in the California Sierra Nevada Range, two maternity roosts were discovered in basal hollows of giant sequoia trees, two in snags of sugar pine, and two other roosts were discovered in snags of ponderosa pine (Pierson et al., 2006). Roosts held one to 29 bats, and one female tracked for five days changed roosts daily (Pierson et al., 2006).

Habitat characteristics of thirteen fringed myotis maternity colony sites in Colorado and one site in northern New Mexico were investigated by Hayes and Adams (2015), including roosts discovered by radio tracking seven females. No roosts were in trees or snags. Ten sites were on faces of rock outcroppings or cliffs, one was in a crevice in a boulder, two were in abandoned mines, and one was in an abandoned cabin. Model selection procedures including four landscape-level variables were used to best describe habitats at nine maternity sites in comparison with randomly selected potential roost sites. The top three models were all competitive, and involved combinations of variables that measured grade (% slope), aspect, elevation, and distance to water, with a model involving just grade and aspect having the highest weight (Hayes and Adams, 2015). Maternity sites had steeper grades (mean 43% slope) and southerly aspects. Estimated maternity colony sizes in rock structures based on visible clusters ranged from four to 30 individuals, whereas colonies in each of two abandoned mines numbered about 100 bats. Based on radio tracking and other supportive observations, Hayes and Adams (2015) suggested that this species showed high daily and long-term (multiple years) fidelity to maternity roost sites in their study regions. In western Colorado, Neubaum (2017) radio tracked two lactating females to five roosts, all located in crevices in high cliffs.

In the Black Hills of South Dakota, 15 fringed myotis (13 reproductive females) tracked from one to 10 days used 36 roosts (27 in rock crevices, nine in tree snags), averaging 1.8 days per roost, with exit counts ranging one to 27 bats (Cryan et al., 2001). Only two bats roosted in trees (both lactating females), one of which also roosted in rock crevices; other tracked bats did not switch between trees and rock crevices (Cryan et al., 2001). Roosts in trees were in cavities or cracks of ponderosa pine snags, with none under exfoliating bark (Cryan et al., 2001). Roost trees were greater in diameter but did not differ in height compared to randomly selected snags; numbers of snags were greater in roost plots than in randomly selected plots and more roosts were on south-facing slopes than expected (Cryan et al., 2001). The rock crevices were in sandstone and limestone boulders and cliff faces with southern exposures. Females roosted in deeper crevices (greater than 25 centimeters) than males. Most rock roosts were in rock ridges or canyons at the ponderosa pine and oak/juniper ecotone, where snags were also plentiful (Cryan et al., 2001).

Fringed myotis also have been observed roosting in both rock outcroppings and in trees in ponderosa pine forests in far northwestern Arizona (Herder and Jackson, 2000). However, Rabe et al. (1998a) found that 15 adult females followed by radio tracking during the reproductive season in northern Arizona roosted only in ponderosa pine snags, with one exception roosting in a Douglas fir snag. Fringed myotis females ($n = 16$) radio tracked in east-central Arizona ponderosa pine forest roosted in 17 snags and two live trees of five species and one rock roost, with mean colony sizes of 63 bats observed in exit counts (range 26–86; Saunders, 2015).

In the Jemez Mountains of New Mexico, seven adults (six lactating females) were tracked for three to 18 days and used 11 roosts: all roosts were in rock crevices or solution cavities located nine to 23 meters high on cliff walls, most facing southeast (Bogan et al., 1998). Colony sizes varied from four to 162, averaging 66 bats (Bogan et al., 1998). In piñon-juniper woodlands of the Gallinas Mountains of New Mexico, Chung-MacCoubrey (1996) found maternity colonies numbering 30–40 individuals roosting in ponderosa pine snags or live ponderosa pines with long, vertical cracks and loose bark. These trees were in isolated stands or "stringers" along arroyos, and at the pinyon-juniper woodland-ponderosa pine forest ecotone. Year-to-year reuse of roosts in trees was documented (Chung-MacCoubrey, 2003).

Warm Season Roosts in Caves, Mines, Buildings, and Bridges: Fringed myotis will also roost in caves and mines during warm seasons. Nursery clusters numbering 400–500 in each cluster were noted in "several rooms" of a cave in Chihuahua, Mexico near Big Bend National Park (Easterla, 1973:41). A "semi-dormant" clump of 18 adult males was observed in mid-August in a mine tunnel in oak-walnut-sycamore habitat in the Huachuca Mountains of southeastern Arizona, and a colony of adult females and young were found at a separate mine at the lower edge of the oak belt; these bats were also taken at the lower edge of the pine belt (Hoffmeister and Goodpaster, 1954). A colony of about 250 females and young was observed in a cave in the Chiricahua Mountains of Arizona in 1954, with about 50 seen at this location the following summer (Cockrum and Ordway, 1959). About 2,000 individuals were observed roosting during summer in an abandoned mine in the Santa Rita Mountains of Arizona, with other colonies also reported using other abandoned mines during summer in the same region (von Bloeker, 1967). Two colonies of unspecified function numbered up to 121 individuals in one Arizona cave and up to 71 bats in a second cave during summer (Arizona Game and Fish Department data cited in Ellison et al., 2003).

Banding records of fringed myotis from roosts in Mohave County, Arizona indicated strong year-to-year fidelity to colonial roosts in abandoned mine tunnels (Cockrum et al., 1996). Altenbach and Sherwin (2002) report a decline of a maternity colony at a New Mexico cave from over 500 adult females in 1990 to zero bats in 2001, while an abandoned mine about eight kilometers distant became occupied instead, apparently through displacement of the colony in the cave by disturbance. An abandoned mine with unusually cool temperatures was used as a roost during June when females were pregnant, and this use was suggested to be a possible mechanism to induce an embryonic diapause (Altenbach et al., 2000); they are known to give birth in maternity colonies with a high degree of synchrony among individuals (O'Farrell and Studier, 1973). In late summer and early fall, dormant bats were found roosting solitarily or in very small groups in several abandoned mine tunnels in Mohave County, Arizona (Cockrum et al., 1996).

Fringed myotis will also roost in buildings and bridges during warm seasons. The species was discovered and named in part based on specimens from the attic of an adobe building that housed a maternity colony at Old Fort Tejon, California in 1891 (Miller, 1897). This building was re-visited in 1904, but the colony was absent (Grinnell, 1918); in 1945, three were captured at 0300 h returning to the building to roost (Dalquest and Ramage, 1946). A colony of about 50 adults and young was documented using the roof of a building near Angwin, Napa County, California in July 1945 (Dalquest 1947a), and smaller numbers were reported from attics in Kern, Santa Cruz, and San Mateo counties (Dalquest, 1947b). A maternity colony of about 200 was reported from the attic of a building in northern New Mexico at about 2,040 meters elevation during late June 1967 (Studier, 1968). This colony was later reported to consist of 1,000 to 1,200 individuals (nearly all adult females and young) in 1970 (O'Farrell and Studier, 1975). Bridges were found to house both diurnal- and night-roosting bats in the central Sierra Nevada of California (Pierson et al., 2001). Only a single transient individual was reported roosting under a bridge over the Rio Grande in southern New Mexico, despite multiple surveys of 17 bridges over a two-year period when many individuals of several other species were recorded (Geluso and Mink, 2009).

Night Roosts: Fringed myotis are well known to use night roosts in caves, buildings, mines, and other sites not used as diurnal roosts. As examples, they were documented night-roosting in buildings at two locations in Kern County, California (Dalquest and Ramage, 1946; Dalquest, 1947a), at cabins in Santa Cruz and Monterey counties (Dalquest, 1947b), and at a barn in Colorado (Barbour and Davis, 1969). They also were reported night roosting in a cave in Oregon (Albright, 1959) and a mine in Arizona (Barbour and Davis, 1969). Small numbers of night-roosting individuals also have been reported under bridges in northern California that were used as night roosts by much larger numbers of other species (Pierson et al., 1996b).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Three females each had single embryos in McKittrick Canyon in the Guadalupe Mountains National Park, Texas, (LaVal, 1973). Two females taken in the San Luis Mountains near the New Mexico-Sonora border had one embryo each (Miller and Allen, 1928; Anderson, 1972), as did three females taken at Wind Cave National Park in South Dakota (Turner, 1974). Two females taken near Colorado Springs had one embryo each (Barbour and Davis, 1969), as did two females taken in Jalisco (Watkins et al., 1972), two females from Chihuahua (Barbour and Davis, 1969; Anderson, 1972), and one female from Chiapas, Mexico (Carter et al., 1966). One female taken in the Trans-Pecos region of Texas had a single embryo (Yancey, 1997).

Reproductive rates of female fringed myotis captured over water were 57% ($n = 37$) during a three-year period (including drought and non-drought years) in the Jemez Mountains of New Mexico (Bogan et al., 1998). Thirty of 31 (97%) females examined based on captures at roosts and over water in the Mogollon Mountains of western New Mexico and eastern Arizona during June and July 1957 to 1961 were reproductive (C. Jones, 1964), and “about 90%” of a likely 51 females captured at a maternity roost in Las Vegas, New Mexico during 1970 were reproductive (O’Farrell and Studier, 1975:370). In northern Arizona, 34 of 52 females (65%) taken over water in ponderosa pine forest were reproductive during 1993–1995 and seven of 13 (54%) females captured over water in ponderosa pine-oak forest were reproductive in 1994–1995 (Morrell et al., 1999). Twenty-two of 26 (85%) females captured over water during summers 1989–1996 in the Black Hills of South Dakota were reproductive (Cryan, 1997). Forty-four of 48 females (92%) taken both at maternity roosts and over water in Big Bend National Park, Texas were reproductive during 1967–1971 (Easterla, 1973). Fifty-six of 81 females (69%) captured over water in south-central Oregon and Washington during 2001–2003 were reproductive (Lacki and Baker, 2007).

At Mesa Verde National Park in southwestern Colorado (including a drought year), five of 11 (45%) females captured over water during 2006 and 2007 were reproductive (O’Shea et al., 2011a). In Boulder County, Colorado, 137 of 155 (88%) adult females captured mostly over water during multiple years (1995–2009) were reproductive (Hayes, 2011). However, elevation biases were not taken into account in this estimate (non-reproductive females occur at higher elevations than reproductive females in this region [Hayes and Adams, 2015]), and reproductive females may be more likely to be captured because they drink more frequently when lactating (Adams and Hayes, 2008), and are heavier when pregnant. The proportion reproductive for the cumulative total females taken over water over all U.S. locations and years was 75% (282 of 375 bats).

We are unaware of any published literature with quantitative data concerning age at first reproduction or inter-birth intervals in fringed myotis.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Little is known about causes of mortality in fringed myotis. Neonatal mortality is low, estimated at about 1% for a colony studied in an attic near Las Vegas, New Mexico (O’Farrell and Studier, 1973). Predation by house cats has been reported (Hoffmann et al., 1969), as has accidental drowning in a rain barrel (Bailey, 1931). Helminths, coccidial protozoans, and ectoparasites have been documented but no associated mortality reported (for example, Cain and Studier, 1974; Whitaker and Wilson, 1974; Duszynski et al., 1999; Ritzi et al., 2001). Deaths due to rabies occur (for example, Constantine, 1979, 1988; Constantine et al., 1979), but the presence of rabies-virus-neutralizing antibodies in individuals sampled in Colorado (Bowen et al., 2013) suggests some degree of immune resistance to this virus. White-nose syndrome has not been reported for this species. Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with anti-fungal properties on wings of these bats and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America.

Excessive collecting no doubt had impacts on survival in local populations in the past (for example, Easterla, 1973). Maximum longevity has been reported as at least 18 years (Tuttle and Stevenson, 1982).

Population Trend: Few data on population trends in this species are available. Ellison et al. (2003) analyzed counts at two summer colonies in Arizona but found no evidence of trends, whereas counts at one hibernaculum used by small numbers of fringed myotis decreased from 1969 to 1992.

Weller (2008) evaluated sampling design considerations for use of occupancy estimation models to assess population status and habitat associations of this species in the Pacific Northwest. Occupancy was determined using captures in mist nets and echolocation recordings during four surveys at 51 carefully selected sites in Washington, Oregon, and northern California, and estimated based on a series of habitat models (including categories for successional stage and conservation reserve status) that were ranked using Akaike's Information Criteria. Fringed myotis were detected at 21 sites (observed occupancy of 0.412). Model-averaged detection probability estimates were 0.252 ± 0.07 (SE), the second lowest of eight species sampled, and overall occupancy estimates were 0.605 ± 0.16 (SE) using the best ranking model. Point estimates of occupancy were higher in late-succession/old growth habitat (Weller, 2008). Increased precision would have been possible with greater numbers of surveys per site and greater numbers of sites, or perhaps by increasing the numbers of identifiable echolocation calls recorded (Weller, 2008).

Species dynamic distribution models were constructed using Bayesian hierarchical modeling techniques for 12 species of bats in Washington and Oregon based on an eight-year monitoring program; bat activity was sampled with mist nets and acoustic detectors, and the analysis accounted for detectability and annual turnover in bat occurrence (Rodhouse et al., 2015). This was the only species that showed a decline in occurrence probabilities with time and that was considered to be at risk (Rodhouse et al., 2015).

MANAGEMENT PRACTICES AND CONCERNS.— In studies of several species of bats (including *M. thysanodes*) roosting under loose bark or in lightning-caused cracks of snags in northern Arizona, Rabe et al. (1998a) recommended measures to help recruit snags with loose bark as bat roosts. They suggested that forest management should retain large trees that die in place, thin stands of small trees to allow faster development of larger trees, and kill live large trees in areas of low snag density to hasten roost development. Prescribed fire (but with protection of existing snags) also may help promote development of future snags (Rabe et al., 1998a).

Analysis of roost-tree characteristics for fringed myotis in old growth Douglas fir forests of northwestern California showed they utilize tall snags in early stages of decay within stands with multiple similar roosts (see above); investigators recommended that forest management should retain the tallest dead or dying trees, and retain the oldest live trees within green-tree retention zones for future use as bat roosts (Weller and Zabel, 2001).

In Colorado (where few roosts have been located), available data indicate that trees and snags are much less important for roosting than are rock outcrops and cliff faces (Hayes and Adams, 2015). Therefore investigators recommend future identification and protection of roost sites and nearby water resources, installation of bat friendly gates at sites within abandoned mines, and restricting human activity such as rock climbing or operation of noisy equipment near known rock roosts during the maternity season (Hayes and Adams, 2015). Fringed myotis will accept protective gating at summer roosts in caves and mines (Currie, 2000b; Sherwin et al., 2002). In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that fringed myotis continued using gated mines over the long-term, tolerated various gate designs, and that the landscape location and structural complexity of a mine were better predictors than gate characteristics of whether this species would continue using a site after gating. Evidence also indicated that colonies of fringed myotis respond more positively to culvert gates than other mine-roosting species of concern that have been studied (Tobin, 2016).

Lactating females were found to drink at water sources near their day roosts much more often than non-reproductive females, suggesting that loss of watering areas near roosts (as anticipated with global climate change) may have negative implications for population persistence (Adams and Hayes, 2008). Additional analysis involving mathematical models of how populations of fringed myotis might respond to changing climate, in both Colorado and across western North America, suggested that warming and drying climate conditions will cause declines (Hayes and Adams, 2017).

Myotis velifer — Cave myotis (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2010a, 2011b, 2017): Sensitive Species (Arizona, California, Nevada state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Global Ranking G4 - Apparently Secure.

State Designations: Arizona Game and Fish Department (2012): Species of Greatest Conservation Need Tier 1B. California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. Nevada Department of Wildlife (2013): Species of Conservation Priority. Nevada Department of Conservation and Natural Resources (2015a): Critically Imperiled in Breeding Range. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need.

Description.— The cave myotis (Fig. 33) is the largest myotis in the U.S. The forearm length averages about 42 millimeters, range 37 to 47 (Hayward, 1970; Hoffmeister, 1986; Ammerman et al., 2012a). Body mass of females can measure as high as 18.5 grams prior to hibernation, with a mean mass for males of 14.4 grams and females 15.4 grams (Caire and Loucks, 2010); masses at the end of

Figure 33. Cave myotis, *Myotis velifer* (photo by J. Scott Altenbach).

hibernation typically reach 10–12 g or lower (Twente, 1955a; Caire and Loucks, 2010). Pelage coloration varies from light to very dark brown. The nose is less pointed than in some other species of *Myotis*, and the ears reach only to the tip of the nose when laid forward. The area between the scapulae is typically bare or very sparsely haired.

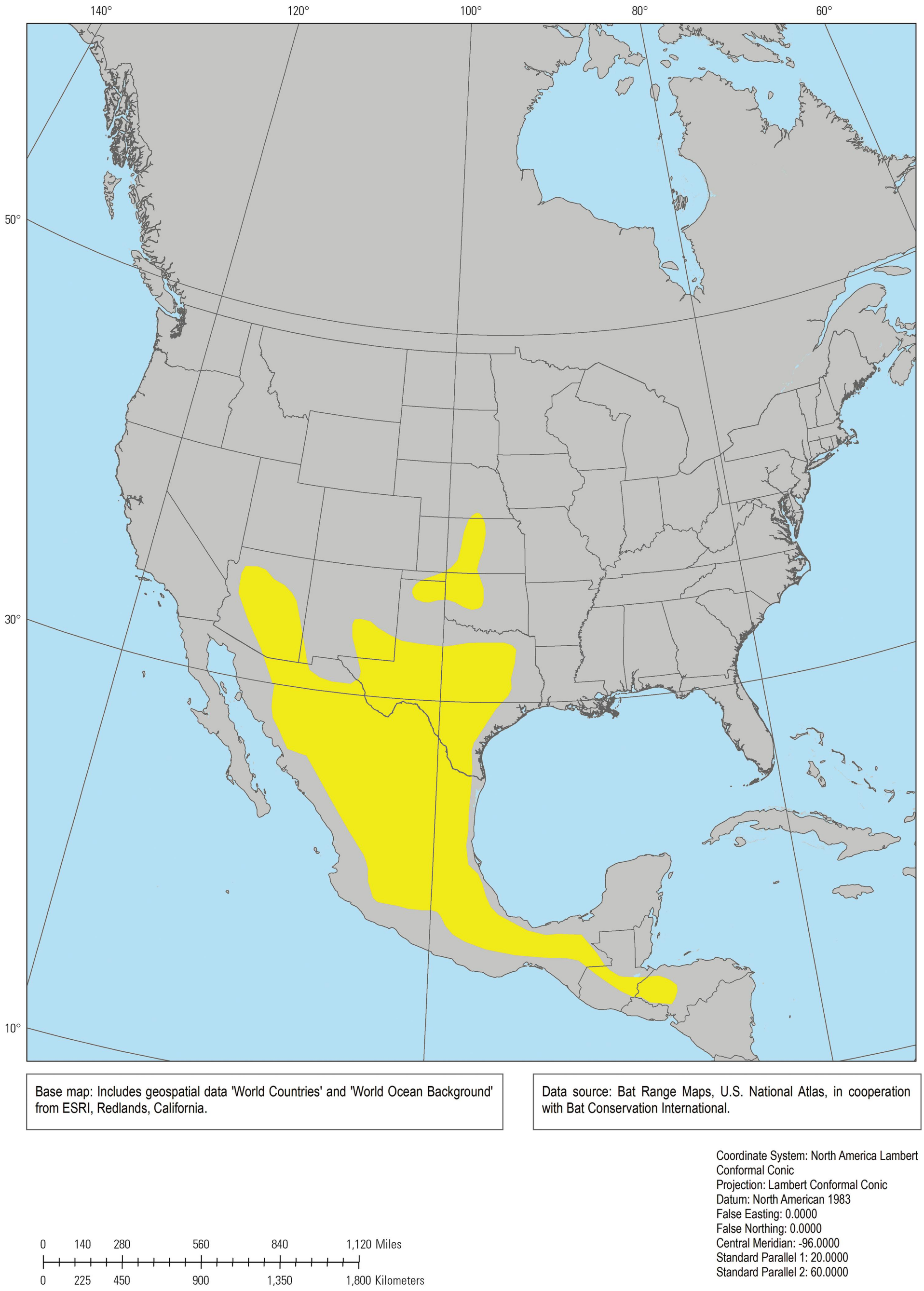
DISTRIBUTION AND SYSTEMATICS.— In the United States, the cave myotis is primarily a lowland species found from southern Kansas to western Texas and southern New Mexico, west to southern Nevada and southeastern California (Fig. 34; Fitch et al., 1981). Five subspecies were listed by Simmons (2005), and the Integrated Taxonomic Information System (2017): *M. velifer brevis, M. v. grandis, M. v. incautus, M. v. magnamolaris*, and *M. v. velifer*. However, Dalquest and Stangl (1984) provided evidence that *M. v. grandis* is a synonym of *M. v. magnamolaris*, and Hayward (1970) and Hoffmeister (1986) considered *M. v. brevis* a synonym of *M. v. velifer*. An additional subspecies, *Myotis v. peninsularis,* was recently designated by Nájera-Cortazar et al. (2015). *M. v. incautus* is found in extreme southeastern New Mexico, southern Texas, and northeastern Mexico. *M. v. magnamolaris* (and synonymous *M. v. grandis*) occurs in southern Kansas, western Oklahoma, and northern Texas. *M. v. velifer* occurs in extreme southern Nevada, in California along the Colorado River, and from central and southern Arizona and extreme southwestern New Mexico southward to Honduras (Fitch et al., 1981). *Myotis v. peninsularis* is found in lower Baja California, Mexico (Nájera-Cortazar et al., 2015). Recent molecular genetic research suggests support for fewer subspecies designations (Parlos, 2008). Fitch et al. (1981) provided a synonymy of past scientific names applied to the cave myotis.

Harris (1974) speculated that the absence of *M. velifer* from the Rio Grande Valley in New Mexico and extreme western Texas may be due to historical competition with the Arizona myotis. Mitochondrial DNA characteristics for this species are available (for example, Zinck et al., 2004). Other common names used in earlier literature include house bat, cave bat, and Mexican brown bat.

HABITATS AND RELATIVE ABUNDANCE.— Cave myotis are typically found in the lower western Great Plains and at lower, warmer elevations in the southwestern U.S. Relative abundances are biased by distance from colony sites, and unless roosting aggregations are near sampling points, they often rank low in relative abundance. This species has been described as abundant and widespread in parts of Mexico during the recent past (Jones et al., 1972).

Southwestern U.S. and Great Plains: *Arizona*: In Arizona, cave myotis occur most commonly in desert areas (Hoffmeister, 1986). Habitats in Arizona can be typically characterized by Sonoran desert vegetation with roosts often within a few kilometers of water, whereas the few winter records are in higher elevation forested areas (Hayward, 1970). In the Huachuca Mountains of southeastern Arizona, summer habitats include low deserts up through oak and pine-oak woodlands (Hoffmeister and Goodpaster, 1954). A mist-netting survey in five riparian canyons in the Huachuca Mountains in 1993 and 1994 found them to rank third in relative abundance among 13 species documented (17 captures out of 145 individuals; Sidner and Davis, 1994). They ranked just tenth in relative abundance (five bats among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim, on the Tonto National Forest in central Arizona (Lutch, 1996). Although 1,342 individuals were banded at six roosts in Mohave County Arizona during 1959–1964, only one was captured in mist nets set over water at multiple locations in the same county, despite captures of 3,458 individuals of 17 other species during the same period (Cockrum et al., 1996). They ranked lowest in relative abundance (1 taken among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) in ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015).

***New Mexico*:** Findley et al. (1975) characterized cave myotis in New Mexico as a desert and



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: Bat Range Maps, U.S. National Atlas, in cooperation with Bat Conservation International.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 34. Approximate distribution of the cave myotis, *Myotis velifer*. Species range is shown in yellow, but also includes southeastern California and southern Nevada.

grassland bat that frequents watercourses. Eight cave myotis were captured among 108 bats of ten species netted over water in Guadalupe Canyon in Hidalgo County, southern New Mexico (ranking third in relative abundance; Mumford et al., 1964). They were the second least frequently captured (a total of three bats) among 1,595 individuals of 20 species taken in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were found in habitats below 1,524 meters (Jones, 1965). None were captured in a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, where 19 species and 1,004 individuals were taken at all three sites; habitats at capture sites ranged from riparian hardwoods at 1,465 meters to pine-spruce-fir forest at 2,620 meters elevation (Jones and Suttkus, 1972). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species with 12 cave myotis, ranking fifteenth in relative abundance (Geluso, 2006, 2017).

Texas and Kansas**:** Cave myotis were reported as uncommon at Big Bend National Park, Texas during 1967–1971 (61 captured among 4,807 bats of 18 species taken at 32 sites, ranking thirteenth), where they were only found in lower elevation vegetation zones (Easterla, 1973). They remained low in relative abundance (ninth in relative abundance among 17 species, with 1.8% of 1,978 bats captured) during a subsequent survey during 1996–1998 that emphasized these lowland habitats but included five vegetation zones; most captures were in shrub desert within canyons (Higginbotham and Ammerman, 2002). This species ranked seventh among 14 (12 out of 542 individuals) captured by mist-net sampling at 108 localities over water in northern Chihuahuan desert habitats described as desert scrub, desert grassland, riparian, and juniper roughland at Big Bend Ranch State Park, northwest and upstream of the national park, in the Trans-Pecos region of Texas (Yancey, 1997).

Cave myotis were low in relative abundance (two among 1,329 individuals in 12 species, ranking eleventh) captured in mist nets set over water at Palo Duro Canyon State Park in the Texas Panhandle, where habitats consisted of mesquite (*Prosopis glandulosa*)-juniper associations, grasses, and cacti and a riparian zone of cottonwood (*Populus deltoides*) and salt cedar (*Tamarix ramosissima*) set within sandstone, shale, and limestone canyon walls that included caves (Riedle and Matlack, 2013). Echolocation activity of this species was sampled in the urban environments of Waco, Texas (Li and Wilkins, 2014). Habitats used differed from those of several other species of local bats but were similar to those of big brown bats, favoring areas with the presence of water and low-density residential development (Li and Wilkins, 2014). In Kansas, cave myotis are only known from the Gypsum Hills region of the south-central part of the state, with some expansion of the distribution to adjacent areas by adapting to roost in buildings rather than caves (Sparks and Choate, 2000).

Foraging and Dietary Analysis.— In Kansas, *M. velifer* were characterized as feeding at heights of four to 12 meters earlier in the night, but at lower heights just before dawn (Kunz, 1974). Habitats utilized in this region included prairies and juniper-elm associations in canyons and hillsides, with riparian woodlands utilized along floodplains. On warmer nights, they foraged in open areas adjacent to forested areas and above canyons but fed close to dense vegetation on cooler nights; they foraged in light rain but returned to roosts when precipitation was heavy (Kunz, 1974). Most foraging took place early after emergence, with a secondary period of foraging activity before dawn, although when first becoming volant the young foraged in a single, concentrated time period (Twente, 1955b; Kunz, 1974). Night-roosting behavior increased later in summer (Kunz, 1974). Peak food consumption in females reached 30% of body mass nightly and occurred in summer just prior to weaning of young (Kunz, 1974).

Shortly after emergence, light-tagged individuals in high rolling plains and deep canyons of western Oklahoma foraged while dispersing down canyons primarily at six to 15 meters above short stream vegetation or above taller cottonwoods at 15–30 m; most foraging episodes consisted of dipping and darting from side to side while flying in eight by 45 meters oval flight paths (Caire et al., 1984). In Kansas, cave myotis were reported to feed over high prairies at dusk, later moving down to river valleys (Hibbard, 1934). Individuals from colonies observed in the Riverside Mountains of southern California appeared to forage mainly over the floodplain of the Colorado River, utilizing dense linear stands of catclaw acacia, mesquite, tamarisk, and screw-bean bordering oxbows as well as scattered thick patches of vegetation elsewhere, often feeding within a few centimeters of the foliage and in small spaces between plants (Vaughan, 1959).

This species has been described as an opportunistic feeder in south-central Kansas, where beetles were the major prey (37% of food items), followed by homopterans (18%), dipterans (14%), and lepidopterans (12%); size of prey varied from less than four to 20 millimeters (Kunz, 1974). Opportunistic feeding also was observed in central Arizona, where these bats foraged on ephemeral swarms of flying ants (*Pogonomyrmex* sp.; Vaughan, 1980). In southern Arizona, they primarily consumed microlepidopterans, but at certain times weevils taken over agricultural fields formed the bulk of the diet (Hayward, 1970). Microlepidopterans about 10 millimeters in length were the predominant items found in stomach contents of 15 of 22 specimens from Arizona and Sonora, although small (four to 13 millimeters) beetles and weevils, dipterans, cicadellids, and neuropterans were also found (Ross, 1964, 1967). Food habits of adult females roosting in two caves and three barns during summer 2004 in the Red Hills of southern Kansas apparently did not differ between the two roost types, despite likely differences in thermal environments and consequent energetic requirements (Marquardt and Choate, 2009). The primary prey species in decreasing proportional volume were coleopterans (particularly scarabaeids), lepidopterans, dipterans, and hemipterans (Marquardt and Choate, 2009), similar to earlier findings of Kunz (1974).

ROOSTING HABITS.— Cave myotis are colonial, and roost in caves, old mines, and culverts, as well as in bridges and occasionally buildings (Grinnell, 1914; Hoffmeister and Goodpaster, 1954; Constantine, 1961a; Hayward, 1963, 1970; Anderson, 1972; Kunz, 1973). They often retreat into cracks and crevices within roosting sites.

Winter Roosts: Studies of cave myotis in winter hibernacula have taken place in caves of central Kansas, northwestern Oklahoma, and northwestern Texas, some of which also may be used as summer colony sites (Twente 1955a,b; Tinkle and Milstead, 1960; Tinkle and Patterson, 1965; Dunnigan and Fitch, 1967; Caire and Loucks, 2010; Humphrey and Oli, 2015). In northwestern Texas during 1957–1963, they hibernated in multiple caves in colonies of about 1,000 to 5,000 individuals at locations within 100 kilometers of their maternity colonies (Tinkle and Patterson, 1965). Hibernating bats had fidelity to the cave where originally banded (80% of recoveries) or groups of caves within a local area (17%), with few making longer movements to other areas with hibernacula: less than 2% of over 10,000 banded bats made such major movements, averaging 89 kilometers with a maximum of 145 kilometers (Tinkle and Patterson, 1965). Local movements among caves within eight kilometers of each other within winters were commonly observed, thought to be due to changing conditions of temperature, humidity, and air currents (although disturbance by investigators may also have been a factor). Within caves, bats frequently changed positions during winter and moved among clusters on ceilings as well as to positions within groups in deep crevices; thermal regimes were cool and less fluctuating in these crevices, and groups of bats tended to be more stable in composition within crevices than on ceilings (Tinkle and Patterson, 1965). Caves with coldest temperatures and highest levels of humidity were generally favored as hibernacula. Estimates as high as 46,700 hibernating bats were reported in one cave in northwestern Texas during 1960 (Tinkle and Patterson, 1965). Although peak counts are variable, the Selman

Cave System in northwestern Oklahoma has consistently contained tens of thousands of cave myotis during winter in recent decades (Loucks and Caire, 2007; Creecy et al., 2015).

In southern Kansas and northwestern Oklahoma, cave myotis studied during 1952–1953 moved from caverns used in autumn to other caves used as winter hibernacula, where the largest colony size was about 7,000 bats in a single cave (Twente, 1955a,b). Bats in the latter cave were found in large clusters of about 200, smaller clusters, or as pairs or solitary individuals; some movements of banded bats among hibernacula were noted within the winter season (Twente, 1955a). Areas of caves with cold temperatures and low air circulation were favored, and sizes of clusters increased as the winter progressed (dense clusters of 1,700 bats per square meter were reported); bats dispersed to warmer caves in late March and early April (Twente, 1955b). Winter roosting can occur over water or in damp conditions above cave floors (Hibbard, 1934). Additional studies of use of these and other caves and mines by this species in southern Kansas took place during 1963–1966, and provided additional information on numbers of hibernating bats, sex ratios, and movements, which were mostly local (Dunnigan and Fitch, 1967). Twenty winter roosts in northwestern Oklahoma were studied further during 1966 to 1977, with an emphasis on movements and demography as determined through banding (Humphrey and Oli, 2015). Little movement away from the study area occurred, with 90% of 200 bats marked as juveniles and 81% of 559 adults marked in summer recaptured in the core area caves during winter (Humphrey and Oli, 2015). Banded individuals will switch hibernacula between winters (Humphrey and Oli, 2015).

Populations of cave myotis in Kansas, Oklahoma, and northwestern Texas inhabit the same region year-round (Tinkle and Patterson, 1965; Kunz, 1974; Humphrey and Oli 2015). A single individual was netted over water in the Trans-Pecos region of Texas in late February (Yancey, 1997). In California and Arizona, large overwintering populations are poorly known, and some may move southward into Mexico where hibernation may occur at higher elevations (Fitch et al., 1981). However, Cockrum et al. (1996) speculated that cave myotis from lower elevations in Mohave County, Arizona may move upslope to hibernacula at higher elevations. In southern Arizona, they are thought to move southward with just a few individuals (fewer than 15 bats, rather than colonies) remaining to hibernate in abandoned mines at elevations higher than about 1,825 m, where conditions are wet and air circulation patterns result in temperatures of about eight to 11ºC (Hayward, 1970). Despite records of warm-season colonies in abandoned mines along the Lower Colorado River of southeastern California and western Arizona, only small numbers of overwintering cave myotis have been found in these mines (Brown, 2013). Similarly, only small numbers were found utilizing bridges as roosts during winter in southern Arizona (Wolf and Shaw, 2002).

Warm Season Roosts: Colonies of cave myotis can be found in caves and mines, in buildings (for example, Kunz 1973), and under bridges (for example, Hoffmeister, 1986; Wolf and Shaw, 2002). In Kansas, small, widely scattered transient colonies occur in early spring prior to maternity colony formation, and in autumn prior to the hibernation period (Kunz, 1974). Smaller cluster sizes also have been observed in Arizona during spring and autumn (when torpor is more evident) in comparison with summer, and during spring and autumn they will roost in a wider variety of situations, including buildings, carports, and swallow nests (Hayward, 1970; see also above).

Vaughan (1959) described summer daytime roosts in deserted mine tunnels in the Riverside Mountains of southeastern California, where this species was absent in winter and early spring. They were found in clusters of several to over one hundred in crevices, drill holes, and irregular or hollowed-out areas on the ceilings. Tunnels each contained from several hundred to roughly 1,000 individuals, and these bats were usually most abundant in clusters at the deeper parts of tunnels more than about 20 meters from the entrances.

Maternity colonies may include both males and females, at least up until parturition (Hayward, 1970; Kunz, 1973, 1974), and nursing females may be found nearest entrances in warmest parts of warmer caves and tunnels, particularly those least likely to be disturbed by people (Tinkle and Patterson, 1965; Hoffmeister, 1986). Later in summer males in Kansas were found to roost in cooler caves than females and young, most typically alone or in small groups (Kunz, 1973). Caves used by this species in Kansas during warm months were characterized by low fluctuations in temperatures and relative humidity (which remained at about 100%) whereas roosts in buildings had much greater variation in these climatic factors (Kunz, 1973). Foraging females leave young behind at the roosts during the early night but they soon return to nurse them (Kunz, 1973). Roosting cave myotis in Kansas form clusters that can increase surrounding temperatures by four to 12ºC, and also can significantly increase humidity (Kunz, 1973).

Summer colonies may typically number 2,000–5,000 bats, with a maximum of 15,000 to 50,000 estimated in past surveys (Twente, 1955b; Dunnigan and Fitch, 1967; Hayward, 1970). Although this species is vulnerable to disturbance, the majority of one large (30,000 to 50,000 bats) colony in Kansas occupied a lighted area of an active gypsum mine in the immediate area of a frequently used ore-train track (Dunnigan and Fitch, 1967).

Banded individuals from summer colonies in mines in mountain ranges in southern Arizona showed year-to-year switches among specific mines but had fidelity to a larger area encompassing groups of mines (Hayward, 1970), similar to above findings in the western Great Plains. Within-season shifts in population sizes at specific caves during the maternity period were also noted over a larger geographic area encompassing multiple caves in northwestern Oklahoma, with movements among caves documented through band recoveries (Humphrey and Oli, 2015). Maximum emergence counts at three of these maternity caves were 7,420 bats, 7,179 bats, and 4,620 bats with a maximum of 14,583 bats counted over the full core area; post-lactation peaks in counts were not obvious, suggesting rapid dispersal of weaned young (Humphrey and Oli, 2015).

In Mohave County, Arizona, abandoned mine tunnels used as transient roosts by small numbers of individuals also housed a maternity colony of about 1,000 in mid-summer, but dropped to a single bat by early August (Cockrum et al., 1996). In nearby San Bernardino County, California, an abandoned mine had a seasonal peak count of about 5,000 bats during 2013 (Brown, 2013). Examples of other maternity colony sizes recently reported include 10,000–12,000 bats each in two caves and 8,000 to 10,000 bats each in two barns in the Red Hills of southern Kansas during 2004 (Marquardt and Choate, 2009), and 700–800 in an abandoned mine on the Arizona side of the Havasu National Wildlife Refuge (Brown, 2013). (See also “**Population Trend**” below.)

Cave myotis may appear at nursery colony sites in caves on the Edwards Plateau in Texas in early February during warm years (Raun and Baker, 1958). In Baja California, Mexico, a colony of about 5,000 females and young was reported from a cave, a male colony of about 25 bats were reported from a mine tunnel, and about 100 females and young occupied a doorsill of an abandoned adobe house (Jones et al., 1965).

Cave myotis are well-known to share roosts with Brazilian free-tailed bats and Yuma myotis in summer (Stager, 1939; Cockrum et al., 1996; Brown, 2013). Roosts are often located near water, and they have been observed moving directly to water to drink after emergence (for example, Bailey, 1931; Twente, 1955b).

Cave myotis will roost in nests of swallows. Individuals have been observed roosting solitarily in 18 of 57 barn swallow (*Hirundo rustica*) nests in Texas during late August (Jackson et al., 1982) and roosting in twos and threes in abandoned cliff swallow (*Petrochelidon pyrrhonota*) nests in western Texas during late September (Ritzi, 1999). They were found in both cliff and barn swallow nests in six counties in south-central Texas in all months of the year except January, with a maximum of 14 found in two nests (Pitts and Scharninghausen, 1986). Nine individuals were found in a southern Arizona cliff swallow nest in September (Hayward, 1970). They also have been found roosting in nests of cave swallows (*Petrochelidon fulva*) in twos and threes during December in central Texas (Ritzi et al., 1998).

Night Roosts: Cave myotis often utilize night roosts, which may differ in location from diurnal roosts, after filling their stomachs early in the night. Night roosts may be in caves, mines or buildings, and bats may night roost as singletons or in smaller clusters than they usually form in the daytime. They also may rest in trees for brief periods at night (Caire et al., 1984). This species will share night roosts with other species of bats (Barbour and Davis, 1969; Easterla, 1973).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Copulation occurs in autumn and winter, with sperm storage followed by ovulation and fertilization in spring. Single embryos were found in each of 36 pregnant females sampled in Arizona (Hayward, 1961, 1970) and 39 females sampled from locations in Texas and Arizona (Krutzsch, 2009). One young is born annually in early summer in Kansas (based on 43 dissections with single embryos), with most females giving birth fairly synchronously over a compressed period of about two weeks (Kunz, 1973). In Oklahoma, the parturition period lasts about four weeks, from approximately the second week of June through the second week of July, with the majority of births occurring in the middle two-week period, similar to Kansas populations (Loucks and Caire, 2007). Two pregnant females brought into captivity in Kansas each produced singletons (Twente, 1955b), and four females from Kansas each had single embryos (Dunnigan and Fitch, 1967). Two females from Arizona each had single embryos (Cockrum, 1955), as well as one female taken in Jalisco, one taken in Chihuahua, one taken in Sinaloa, and nine taken in Durango, Mexico (Jones et al., 1962; Jones, 1963; Bradley and Mauer, 1965; Watkins et al., 1972). Twinning also can occur, with five of seven females examined in southern New Mexico having a single fetus and two females having twins (Geluso and Geluso, 2004). Females become sexually mature in their first year of life in Texas (Krutzsch 2009), and all of 39 females banded as juveniles were found to be pregnant or lactating the subsequent year at a maternity roost in Kansas (Kunz, 1973). The sex ratio of 474 volant young at an Oklahoma maternity roost was 1:1 (Loucks and Caire, 2007).

Natality at maternity colonies was nearly 100% in a Kansas study (Kunz, 1973) and 96% in Oklahoma (Humphrey and Oli, 2015). Seven bats were reproductive in a sample of 10 females (70%) mostly taken over water at Big Bend National Park in Texas (Easterla, 1973). Nine of ten females (90%) collected at unspecified locations in Durango, Mexico, were reproductive (Jones, 1963). Four of six females examined in Kansas in 1964 were pregnant (Dunnigan and Fitch, 1967).

Survival: In a metapopulation covering multiple caves in a 186–square-kilometer core area studied in northwestern Oklahoma during the 1960s and 1970s, estimated apparent survival was lowest the first six months post-weaning (Humphrey and Oli, 2015), a pattern similar to that seen in other species of bats (for examples see reviews in O'Shea et al., 2004, 2010). Survival increased over the first half of the lifespan, then declined (Humphrey and Oli, 2015). Apparent survival estimates for the northwestern Oklahoma population studied by Humphrey and Oli (2015) varied by sex and time, with females having higher apparent survival than males, and annual rates ranging between about 0.5 and greater than 0.70 in unknown-age females, depending on year.

Minimum-number-alive survival rates (biased by banding effects in a declining population) in a northwestern Texas study conducted during 1957–1963 suggested a maximum mortality of about 80% in the first year of life, annual survival of 0.47, and that most bats in the population were less than three years old with a maximum age of six years (Tinkle and Patterson, 1965). These survival estimates appear unsustainable (see review in O'Shea et al., 2011c) but possibly may include permanent emigration, banding-caused mortality (Hitchcock, 1965; O'Shea et al., 2004), or other unknown effects. Longevity records range from at least seven years (Paradiso and Greenhall, 1967; Hayward, 1970) to 10–12 years (Hayward, 1970; Cockrum, 1973).

Mortality Factors: Infant mortality is probably highest during the first few days of life preweaning (Kunz, 1973). Raun (1960) reported a mysterious finding of up to several thousand mummified carcasses and other remains of cave myotis at Valdina Farms Sinkhole, Medina County, Texas, in 1959, but with no apparent cause of death. Cockrum (1952) noted six or seven mummified individuals hanging from the ceiling of a Kansas hibernaculum, also with no apparent cause of death. Known mortality factors include deaths due to flooding of caves (high water marks up to ceilings in roosts), collapses of rock ceilings above roosting bats (447 dead bats noted in a single collapse), subfreezing temperatures (34 dead and dying bats noted in one cave), and human disturbance and vandalism at roosts (Humphrey and Oli, 2015). One was discovered killed from collision with turbine blades at a wind energy facility in northwestern Oklahoma (Piorkowski and O'Connell 2010).

Predation is well documented and predators include hawks, owls, snakes, wood rats, skunks, foxes, and ring-tailed cats (*Bassariscus astutus*; Cockrum, 1952; Twente, 1954; Hayward, 1970; Fitch et al., 1981). Raccoons prey on hibernating cave myotis, with remains of 14 found in a single raccoon scat by Twente (1955a), who also reported predation on both adults and young by rat snakes (*Pantherophis* sp.) in Kansas and Oklahoma during summer. Predation by rat snakes in Kansas was previously reported by Hibbard (1934), and a California lyre snake (*Trimorphodon lyrophanes*) was reported with a cave myotis in its stomach (Stager, 1942).

Ectoparasites and endoparasites have been recorded (Eads et al., 1957; Jameson, 1959; Cain, 1966; Nickel and Hansen, 1967; Whitaker and Wilson, 1974). Sparks and Choate (2000) summarized the literature on parasites of cave myotis and reported multiple species of ectoparasites, cestodes, trematodes, and nematodes. An updated summary of endoparasites was reported by McAllister et al. (2007), and more recent documentation of ectoparasites also has been made (Ritzi et al., 2001), but to our knowledge no cases of mortality from parasites have been reported for this species.

Rabies infections occur in cave myotis (Constantine, 1979; Caire et al., 2014), and a new gammaherpes virus has been found in tissues of a sampled individual (Shabman et al., 2016; Host and Damania, 2016). Nineteen forms of bacteria have been isolated from body surfaces of this species from Oklahoma hibernacula, but none were considered pathological (Zanowiak et al., 1993).

The occurrence of environmental contaminants in this species has been studied, but without conclusive evidence of direct mortality. Thies and Thies (1997) sampled a summer colony at Eckert James River Cave in Texas in 1993 for residues of organochlorine pesticides and metabolites and PCBs. These bats had low concentrations of organochlorine pesticides and metabolites in carcasses and brains, with DDE below those in Brazilian free-tailed bats roosting in the same cave system and far below any suggestive of poisoning. The exposure to cholinesterase-inhibiting pesticides in the diet of a Texas population was verified by the presence of trace quantities of organophosphates in guano (Land, 2001). Guano also was analyzed for eight toxic elements in the Texas study, with lead found at relatively high concentrations in samples from one cave (Land, 2001). King et al. (2001) reported unremarkable concentrations of 17 potentially toxic elements in five individuals collected near Roosevelt Lake, Arizona in 1998. They also found no organochlorines other than low amounts of DDE in three individuals from the same sample.

The occurrence of white-nose syndrome caused by the fungus *Pseudogymnoascus destructans* has been investigated in cave myotis in western Oklahoma, where the occurrence of the disease was suspected based on positive genetic tests on white-crustal growth sampled from the wings of a single bat in 2010 (Brennan et al., 2015). Cave myotis were sampled each winter at caves in western Oklahoma for the subsequent four years, but no field evidence of the disease was found, and re-testing of the bat examined in 2010 was found to be negative for presence of the white-nose syndrome fungus (Brennan et al., 2015). Antibodies to other fungal agents were detected in blood of 13 of 28 individuals from the region, but evidence for specific exposure to *P. destructans* could not be conclusively demonstrated (Brennan et al., 2015). Similarly, 83 soil samples from about 17 caves used as hibernacula across Oklahoma were negative for evidence of this fungus (Creecy et al., 2015). However, white-nose syndrome was confirmed in a tri-colored bat in eastern Oklahoma during April of 2017 (Oklahoma Department of Wildlife Conservation, 2017) and DNA of the fungus *P. destructans* was genetically detected on three species of hibernating bats, including a cave myotis, in Texas during 2017 (Texas Parks and Wildlife Department, 2017). Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with anti-fungal properties on wings of this species and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America.

Population Trend: Counts made from 1965 to 2004 at 11 hibernacula in the Red Hills of south-central Kansas and northern Oklahoma suggested one colony in decline, three increasing, and seven with no statistically detectable change; count estimates per hibernaculum ranged from zero to 26,500 bats (Prendergast et al., 2010). Ellison et al. (2003) analyzed time-series data for one summer colony and five hibernating colonies that included counts in four or more separate years in four states (Kansas, Arizona, New Mexico, and Texas). Counts at two winter colonies in Texas declined in the 1950s and 1960s, whereas the other colonies showed no significant trends (Ellison et al., 2003). In one study at a cave in Texas, Elliott et al. (2006) reported that estimates made by counting numbers of cave myotis with a stopwatch during emergence in comparison with estimates made based on ceiling-areas occupied and density of roosting bats were within 13% of each other.

Although more recent population estimates are not available, knowledge from local areas in California, Nevada, and Arizona suggests decline (Altenbach and Pierson, 1995; Pierson et al., 1991; O'Shea and Vaughan, 1999; Brown, 2013). Possible movements of colonies to alternate locations were not investigated. However, considerable numbers of bats had been banded at some of these sites, and banding is known to contribute to declines in some bat populations (O'Shea et al., 2004). In the Verde Valley of central Arizona, a colony of about 5,000 individuals present in summer 1972 was absent in 1997, with the absence attributed to increased use of the area by recreationists (O'Shea and Vaughan, 1999). In southern Arizona, Hayward (1961, 1970) reported large reductions at warm-season colonies in three mines, thought to be due to disturbance, including a drop from 20,000 in 1953 to 200 in 1959 at a single site. The only known colony of this species in Nevada, about 70 bats including females, was discovered in a mine in 1961 (Cockrum and Musgrove, 1964b); only 12 were seen in 2001 (Brown, 2013). Four abandoned mines in the Riverside Mountains of the lower Colorado River Valley in California known to have maternity colonies numbering in the thousands during the 1930s-1950s (Stager, 1939; Vaughan, 1959) were revisited during the 2000s and only two were found to have maternity colonies, with numbers present much lower than earlier estimates (Brown, 2013).

Contemporary published estimates of range-wide population size are unavailable. However, there are published rough estimates for various regions and colonies made in past decades that would provide useful comparisons should future characterizations of population size and trends be made. Hoffmeister and Goodpaster (1954) reported a colony of about 10,000 cave myotis in summer 1949 at Canelo Cave in the Huachuca Mountains of southeastern Arizona. Hayward (1961, 1970) reported several colonies at various southern Arizona locations during the 1960s that varied from about 50 to 15,000 bats and suggested a summer population of 500,000 cave myotis in the region around 1960. Tinkle and Patterson (1965) reported that two of their largest hibernating colonies sampled in northwestern Texas during 1960 held 46,700 bats and 2,819 bats. During 1970, the number of adults of this species in Kansas was estimated at 50,000 by Kunz (1974). This number is somewhat lower than estimates of "between 50,000 and 75,000 individuals" in a gypsum mine in the main part of the distribution in Kansas made during the mid-1960s by Dunnigan and Fitch (1967:11). Twente (1955a) estimated a summer population of 15,000–20,000 for south-central Kansas and northwestern Oklahoma in 1953. Reisen et al. (1976) reported a hibernaculum with 5,000 bats of this species during winter 1972 in a gypsum cave in Harmon County, Oklahoma, and Caire et al. (1984) estimated a warm season colony of about 1,000 bats in Alabaster Caverns, Woodward County, Oklahoma during 1982, with 5,230 reported in this system during winter 1995 (Loucks and Caire, 2007). Counts at 39 hibernacula in Oklahoma during the mid-1990s ranged from 0 to 39,517 individuals, with 18 caves harboring 1,000 or more hibernating bats (Loucks and Caire, 2007). Recent reports of a large population of cave myotis by Creecy et al. (2015) at a cave system in Woodward County, Oklahoma are comparable to winter population records for the same major hibernaculum 16 years earlier (Loucks and Caire, 2007).

Humphrey and Oli (2015) estimated a winter metapopulation of about 20,000 cave myotis in their northwestern Oklahoma study area during the late 1960s and 1970s, and they suggested that single roosts should not be considered as individual populations because of relatively weak roost fidelity in their study area. Count data for the metapopulation encompassing multiple caves in northwestern Oklahoma showed an apparent 40% decline from 23,850 bats in winters 1967–1969 to 14,200 in 1969–1970, then increased over a four-year period at a rate of 12.5% per year and apparently stabilizing at greater than 20,000 for the final three years of the study; cave flooding was hypothesized as a cause for the decline (see "Mortality" above; Humphrey and Oli, 2015). Loucks and Caire (2007) estimated numbers of bats at 39 hibernacula in Oklahoma during winters 1994–1995 and 1995–1996 with counts at individual hibernacula ranging from zero to 39,517. Totals for hibernacula counted in 1994–1995 were 63,285 bats, with a total of 34,718 bats at a somewhat different set of hibernacula counted in 1995–1996 (Loucks and Caire, 2007).

Sex-ratio estimates for cave myotis vary with sampling and depend on time of year, geography, and roosting patterns (Twente, 1955a; Tinkle and Milstead, 1960; Tinkle and Patterson, 1965; Hayward, 1970; Loucks and Caire 2007; Humphrey and Oli, 2015). Variation in adult sex ratios were reviewed in detail by Loucks and Caire (2007), Tinkle and Milstead (1960), and Tinkle and Patterson (1965), who examined a number of hypotheses that may account for this variation.

Population Genetics: Estimates of mean heterozygosity based on allozyme variation at 17 loci in 116 cave myotis sampled at two locations in Texas and a mine in Pima County, Arizona were high (0.144, means of separate populations ranging 0.101 to 0.163 and differing significantly among locations), indicating high genetic variability (Straney et al., 1976). Mitochondrial DNA analysis of 103 bats from Texas, Oklahoma, and the Colorado River region along the Arizona-California border suggest high haplotype diversity (0.965 ± 0.009 SE) and somewhat low nucleotide diversity (0.013 ± 0.006 SE) across all regions combined, with inconclusive evidence for population bottlenecks; nuclear DNA analysis of 192 bats suggest little genetic structuring of the populations sampled (Parlos, 2008).

Management Practices and Concerns.— In California, old mines provide the only currently known sites for colonies of cave myotis (Pierson et al., 1991; Altenbach and Pierson, 1995). Disturbance by people can lead to reductions in populations, as noted for the three mines in Arizona visited by researchers in the 1950's (Hayward, 1970). In Oklahoma, Humphrey and Oli (2015) reported that nursery colonies of this species were much more sensitive to disturbance than were colonies of other species of *Myotis*. Disturbance and banding studies also have been associated with large declines in populations at hibernacula in northwestern Texas (Tinkle and Patterson, 1965).

A hibernating colony averaging over 1,500 of these bats at Torgac Cave on the Roswell Resource Area of the Bureau of Land Management in New Mexico responded favorably to seasonal closures against people and bat-friendly gates (Jagnow, 1998). Protection of colony sites at abandoned mines through utilization of gates or other bat-compatible closure methods has been undertaken by the National Park Service at Big Bend National Park, Guadalupe Mountains National Park, and near the Fort Bowie National Historic Site (Burghardt, 2000). One colony site on the Fort Huachuca Military Reservation in Arizona that was previously abandoned by this species increased to over 8,000 bats following installation of protective fencing and a security system (Buecher and Buecher, 2002). Despite such accounts, it also has been suggested that in some areas very large colonies of cave myotis may not readily accept gating of mines (Brown, 2013). In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that cave myotis continued using gated mines over the long-term, tolerated various non-culvert gate designs, and that the landscape location and structural complexity of a mine were better predictors than gate characteristics of whether this species would continue using a site after gating. Evidence also indicated that colonies of cave myotis respond more negatively to culvert gates than other mine-roosting species of concern that have been studied (Tobin, 2016).

Mann et al. (2002) investigated the potential impact of guided public tours on a maternity colony of cave myotis at Kartchner Caverns State Park in Arizona. They quantified behavior of bats indicative of disturbance (vocalizations, activity levels in clusters, landings and fallings) in relation to experimental tour group size, presence of talking, and four levels of light intensity and color. Talking and higher intensity white light produced more disturbance than no talking or lights, with red light and dim white lights having intermediate impacts. Bats also showed greater disturbance when tour groups were closer, and disturbance levels increased as the maternity season progressed. Mann et al. (2002) recommended that no tours be allowed during the maternity season, that efforts be made to minimize disturbance during other times, and that use of the cave by this species be carefully monitored.

NOTES AND COMMENTS.— Kunz (1974) estimated that the population of cave myotis in Kansas alone consumed 16 tons of insects in a single year. These bats tend to emerge early, well before dark, in large numbers but at a slow rate. Females have been observed to retrieve fallen infants from below roosts (Kunz, 1973).

Myotis volans — Long-legged myotis (Family Vespertilionidae)

CONSERVATION STATUS.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). U.S. Forest Service (2005a,b): Sensitive Species. Bureau of Land Management (2009a, 2011b, 2015b): Sensitive Species (Idaho, Montana, Nevada, North Dakota, South Dakota state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Global Ranking G4 - Apparently Secure.

State Designations: Alaska Department of Fish and Game (2005, 2015): Species of Greatest Conservation Need. California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. Nebraska Game and Parks Commission (2011): At-Risk Species Tier II. North Dakota Game and Fish (Hagen et al., 2005; Dyke et al., 2015): Species of Conservation Priority Level III. Oregon Department of Fish and Wildlife (2005, 2008): Sensitive Species, Vulnerable. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need. Washington Department of Fish and Wildlife (2015a): Species of Concern. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier III.

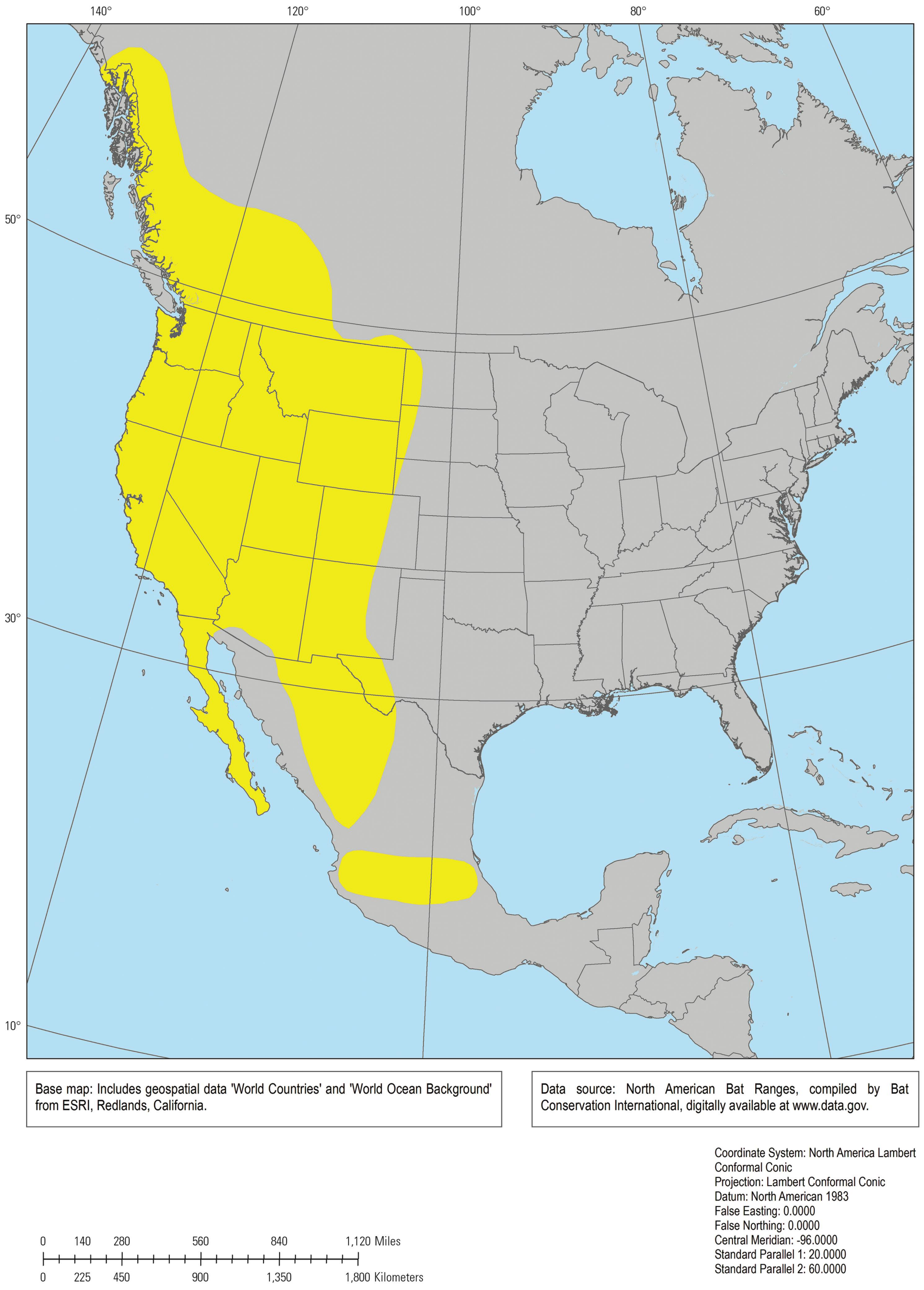
FIGURE 35. Long-legged myotis, *Myotis volans* (photo by J. Scott Altenbach).

DESCRIPTION.— The long-legged myotis (Fig. 35) is an intermediate-sized myotis, with forearm lengths of about 35 to 42 millimeters, body mass ranging 5 to 10 grams, small ears, and a keeled calcar; fur on the underside of the wing extends to the level of the elbow, and is more dense than in little brown (*M. lucifugus*) or Arizona myotis, which lack a keeled calcar (for example, Hoffmeister 1986; Czaplewski, 1999; Armstrong et al., 2011; Ammerman et al., 2012a). Considerable color variation in the pelage can be found among individuals within a given locality (for example, Allen, 1919; Benson, 1949; Vaughan, 1954).

DISTRIBUTION AND SYSTEMATICS.— The long-legged myotis is found in western North America from southeastern Alaska to central Mexico (Fig. 36). The name *Myotis volans* has been assigned to this species for over a hundred years (Goldman, 1914). There are four recognized subspecies (Simmons, 2005): *M. volans volans* (Baja California, Mexico), *M. volans amotus* (found at lower altitudes and deserts in Mexico), *M. volans interior* (the interior western U.S. and Canada), and *M. volans longicrus* (the Pacific Northwest and Canada). Warner and Czaplewski (1984) provided further details and original references on subspecies and a synonymy of past scientific names applied to the long-legged myotis. Molecular genetic variation within the species and relationships with other species of *Myotis* are discussed by Dewey (2006). Other English common names that appear in the literature include hairy-winged myotis, long-legged bat, interior bat, and western little brown bat.

HABITATS AND RELATIVE ABUNDANCE.— Long-legged myotis are found in a variety of western forest types and scrublands, where at many sites they often are among the species most frequently captured in mist nets. They are found over a wide range of elevations from near sea level (Benson, 1949) to high mountain habitats. They are among the few species of western bats found at high elevations, taken at 3,352 meters in the Sierra Nevada of California (Allen, 1919) and 3,500 meters in Colorado (Armstrong et al., 1994), where a carcass was recently recovered at 4,307 meters (Armstrong et al., 2011).

Pacific Northwest, Northern Rocky Mountains, and Alaska: *Oregon, Washington, and British Columbia*: Long-legged myotis were reported to be the most frequently captured species of bat across several forest types in northeastern Oregon (Whitaker et al., 1981). This was the second most abundant (179 captured among 412 individuals) out of eight species of night-roosting bats captured at five bridges in western hemlock (*Tsuga heterophylla*) forest in the Willamette National Forest of Oregon (Perlmeter, 1996). They were of lower relative abundance in surveys over streams and ponds in Douglas fir (*Pseudotsuga menziesii*)-western hemlock forests across the western Cascades in southern Washington and the Oregon Coast Range, ranking fifth among 12 species (nine bats out of 241 individuals; Thomas, 1988). In the same study, echolocation activity of this species was greater in old growth stands than in mature or younger stands, with feeding rates



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 36. Approximate distribution of the long-legged myotis, *Myotis volans*.

higher over streams and ponds than within forest stands (Thomas, 1988). In ponderosa pine forests of the eastern Cascade Mountains in south-central Washington, however, these bats were the second most abundant of 11 species (164 of 1,057 individuals) captured over water (Baker and Lacki, 2004). This species ranked sixth in relative abundance (18 individuals) among 12 species and 958 bats captured over water in the semi-arid Okanagan Valley of southern British Columbia (Woodsworth, 1981). Long-legged myotis ranked third in relative abundance (44 captures) in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water (Fenton et al., 1980).

Montana and Idaho**:** Long-legged myotis were described as the third most common bat and the most common species of *Myotis* among 205 bats netted or shot in the Long Pine Hills and Ekalaka Hills of southeastern Montana, and they were taken over water at beaver ponds and in nearby ponderosa pine forest at elevations of 1,036–1,158 meters (Jones et al., 1973). They ranked seventh in relative abundance among nine species (seven of 231 individuals) of bats captured over water in the Pryor Mountains of south-central Montana (Worthington, 1991). Long-legged myotis also were often captured in forests of multiple types in northern Idaho (ranking most abundant, with 68 of 187 bats of eight species sampled for fecal analysis; Lacki et al., 2007).

Alaska**:** Long-legged myotis were of low relative abundance at the northern periphery of their range in southeastern Alaska south of 59º N latitude, where only three specimens were known through 1995 (Parker et al., 1997). Mist-net surveys in western hemlock, western hemlock-Sitka spruce (*Picea sitchensis*), and mixed coniferous forests of southeastern Alaska during 2005 and 2006 resulted in captures of ten individuals (including reproductive females), ranking them least in relative abundance among 226 bats of four species documented by capture (with all ten captures on Prince of Wales and Wrangell Islands; Boland et al., 2009).

California and Nevada: In the San Gabriel Mountains of southern California, natural history observations and collecting without mist nets revealed the presence of long-legged myotis across a variety of habitats including chaparral, sagebrush flats, ponderosa pine forest (where they were perceived to be most numerous), and the upper limits of Joshua tree (*Yucca brevifolia*) woodlands (Vaughan, 1954). Relative abundances of long-legged myotis were often low during later mist net surveys in California. They ranked sixth among ten species in relative abundance (15 captures out of 284 individuals) in a mist-net survey both over water and within forests (concentrating on groves of giant sequoia trees, *Sequoiadendron giganteum*) in Yosemite National Park in the California Sierra Nevada Range during 2001 (Pierson et al., 2006). Long-legged myotis ranked fourteenth of 17 species (three individuals among 390 bats) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999 (Pierson et al., 2001). They were also rarely taken in mist nets set over water in montane hardwood/conifer habitats along the upper Sacramento River in northern California (Siskiyou and Shasta counties), ranking thirteenth with just two long-legged myotis captured among 1,398 individuals of 15 species documented during 1991–1995 (Pierson et al., 1996b). This species was rarely taken at night roosts under bridges in the latter study area, where just 14 were captured in comparison with 2,132 individuals of nine other species (ranking fifth in relative abundance; Pierson et al., 1996b). They were not reported among 403 bats of 10 species documented in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests (Duff and Morrell, 2007). A survey based on mist netting over water in old growth redwood forest in the Coast Range of northern California resulted in only one individual among 142 bats of seven species (Zielinski and Gellman, 1999).

In eastern Nevada, long-legged myotis were the most abundant and widespread of twelve species of bats (186 among 578 individuals) captured by mist netting over water and captures at abandoned mines and tunnels in six habitat zones (Ports and Bradley, 1996). They ranked second in relative abundance (103 of about 2,000 bats) among 13 species captured foraging in four vegetation zones (ranging from desert scrub to bristlecone-limber pine forests) in the White and Inyo Mountains of California and Nevada, and they were one of only two species of bats captured in the high elevation bristlecone-limber pine forests (Szewczak et al., 1998). This species ranked third in relative abundance at the Nevada Test Site (among more than 2,000 bats of 13 species netted over water), where nearly all (180 of 183) were netted in Great Basin Desert habitat (Hall, 2000). They ranked ninth (five captures among 299 bats of 11 species) in mist-netting surveys over water in west-central Nevada in habitats categorized in four vegetation zones but were only taken in the piñon-juniper woodland zone (Kuenzi et al., 1999).

Southwestern U.S.: ***Arizona*****:** The long-legged myotis was one of the most commonly captured species of bats in ponderosa pine forests on the Coconino Plateau in northern Arizona at elevations ranging from 2,018 to 2,621 meters, where they ranked first among 15 species documented in a 1993–1995 study (400 among 1,673 individuals captured) but were disproportionately lower in relative abundance in mixed ponderosa pine-Gambel oak habitat at slightly lower elevations within the larger study (Morrell et al., 1999). They were the most commonly captured species among 17 species of bats (321 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). Long-legged myotis ranked second in relative abundance (261 captures among 1,441 individuals of 14 species) captured in combined low severity and high severity burn areas (two and three years post-fire) of ponderosa pine forest at 2,345 to 2,686 meters elevation in the Apache-Sitgraves National Forests in east-central Arizona (Saunders, 2015). This species ranked fifth in relative abundance (268 captures among 3,458 individuals) of 17 species netted over water in Mohave County in western Arizona, but it was only captured at sites in or near higher elevation mountain habitats (Cockrum et al., 1996). Long-legged myotis ranked ninth in relative abundance (six bats among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim, on the Tonto National Forest in central Arizona (Lutch, 1996). A mist-netting survey in five riparian canyons in the Huachuca Mountains in southern Arizona during 1993 and 1994 found this species to rank eleventh in relative abundance among 13 species documented (two captures out of 145 individuals; Sidner and Davis, 1994).

New Mexico**:** Long-legged myotis were the second most frequently captured (a total of 226) among 1,595 bats of 20 species taken in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were most abundant in evergreen forest above 2,134 meters (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, they ranked third of 19 species (145 captures among 1,004 individuals) and were taken at all three sites; habitat at capture sites ranged from riparian hardwoods at 1,465 meters to pine-spruce-fir forest at 2,620 meters elevation (Jones and Suttkus, 1972). In the Jemez Mountains of north-central New Mexico, they were intermediate in relative abundance, ranking fifth of 15 species (101 among 1,532 captures) and were netted over water at elevations ranging from 1,753 to 2,774 meters and habitats ranging from ponderosa pine to spruce-fir forests (Bogan et al., 1998). Echolocation activity of this species was commonly detected in riparian, conifer, piñon-juniper, and previously (20 years) intensely burned ponderosa pine habitat in the Jemez Mountains, but it was heaviest in riparian areas (Ellison et al., 2005). This species ranked second in relative abundance (48 among 302 bats of 10–11 species) netted in mostly ponderosa pine habitat at 2,600 to 2,885 meters on Mount Taylor in northern New Mexico (Geluso, 2008).

Chung-MacCoubrey (2005) presented evidence that this species is commonly associated with both piñon-juniper woodlands (the fourth most abundant species taken in mist nets, with 118 captured among 1,222 bats of 10–11 species in the Gallinas Mountains) and ponderosa pine forests (fourth in relative abundance, with 57 captured among 447 bats of seven to eight species in the San Mateo Mountains) in New Mexico. However, reproduction in females was higher in the piñon-juniper woodlands (Chung-MacCoubrey, 2005). At higher elevations in the San Mateo Mountains of New Mexico (ponderosa pine or mixed Douglas fir-blue spruce forests) this species was the second most abundant bat captured in mist nets (506 individuals among 1,390 bats of 10–11 species) during 19 years of sampling over a 34-year period at a natural pool in a canyon floor, elevation 2,573 meters (Geluso and Geluso, 2012). They ranked fourth in abundance (38 captures among 855 individuals) among 16–17 species mist netted over ponds during 1970 at Nogal Canyon, Socorro County, New Mexico, in habitats described as pinyon-juniper, pine-oak woodlands, and mixed-conifer forest at 2,440 meters elevation (Black, 1974). Somewhat farther south, Jones (2016) documented bats captured during surveys of various habitats in the Greater Gila region of Catron, Grant, and Sierra counties of New Mexico; long-legged myotis ranked eleventh in abundance, with seven captures among 282 individuals of 16–17 species and were primarily taken in ponderosa pine forest (Jones, 2016; including data from unpublished reports of others). A survey that took place at 37 sites across several habitat types in much of New Mexico yielded 1,752 bats of 21 species with 131 long-legged myotis, ranking third in relative abundance (Geluso, 2006, 2017).

Texas**:** At Big Bend National Park in Texas, long-legged myotis were rare (six bats among 4,807 captures of 18 species at 32 localities) during 1967–1971 and were taken only at higher-elevation habitats (Easterla, 1973). A subsequent survey during 1996–1998 that emphasized lower-elevation habitats did not result in any captures despite the documentation of 1,978 captures of 17 other species (Higginbotham and Ammerman, 2002).

Central Rocky Mountains and Western Great Plains: *Colorado*: Long-legged myotis were by far the most common species of bat captured in the piñon-juniper woodland and ponderosa pine forests of Mesa Verde National Park in southwestern Colorado (elevations 1,890 to 2,361 meters), with 643 bats captured among 1,996 individuals of 15 species netted over water (O'Shea et al., 2011a). During an earlier study at Mesa Verde in 1989–1994, they were the second most abundant species taken in mist nets (57 bats among 189 individuals of 11 species; Chung-MacCoubrey and Bogan, 2003). They were also the most common species of bat found in forests sampled along the northern Front Range in Colorado (236 bats among 634 individuals of nine species), with nearly all (95%) captures of this species in forests above 2,000 meters (O'Shea et al., 2011b). However, they ranked fifth in relative abundance in surveys across elevations encompassing ponderosa pine and Douglas fir forests farther south in adjacent Boulder County, with 129 captures among 1,398 bats of ten species, but with 58% of all captures involving two species of bats (big brown bats and little brown myotis) that commonly roost in buildings (Adams et al., 2003). These bats were rarely reported (two captures among 506 bats of seven species) in the urban or urbanizing corridor immediately east of the Colorado Front Range (O'Shea et al., 2011b) and in the region in and around Calgary, Alberta (three captures among 1,974 bats of eight species; Coleman and Barclay, 2012).

Long-legged myotis were the most common species (100 captures among 111 bats of four species) at 2,900 to 3,500 meters in spruce-fir forests of the subalpine zone in west-central Colorado, where adult females (likely non-reproductive) dominated samples (Storz and Williams 1996). Maternity colonies have been reported as high as 2,774 meters at abandoned mines in Colorado (Navo et al., 2000). They ranked third most common (57 captures among 546 bats of 11 species) over stock ponds during surveys in piñon-juniper woodland at about 2,100 meters elevation in the Uintah Basin in Moffat County in northwestern Colorado during 1979–1981 (Freeman, 1984). In western Colorado, this species ranked fourth in relative abundance of 16 species (88 among 899 bats) captured at Colorado National Monument and the adjacent McInnis Canyons

National Conservation Area during netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Long-legged myotis ranked fifth in abundance (139 captures among 1,377 bats of 15 species) in mist-netting surveys at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

Utah**:** In the Henry Mountains of southeastern Utah, long-legged myotis ranked third in relative abundance of 15 species (71 captures among 572 individuals), where they were taken between 1,439 and 3,078 meters but apparently moved to higher elevations above 2,000 meters after May (Mollhagen and Bogan, 1997). At Arch Canyon on the Colorado Plateau in southeastern Utah, this species was among the least abundant, with two bats captured among 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016).

Wyoming: Long-legged myotis were the most common species (99 individuals among 246 bats of six species) captured in mist-net surveys over streams and beaver ponds in and near the Medicine Bow National Forest in southern Wyoming, at elevations ranging from 2,133 to 2,896 meters in habitats encompassing lodgepole pine (*Pinus contorta*) and spruce-fir forests (Gruver, 2002). They have been reported at elevations as high as 2,743 meters in northwestern Wyoming (Hoffmann et al., 1969). They ranked fourth among 12 species (26 captured among about 370 individuals) documented by mist netting during 2012 in lower-elevation basin and foothills habitat in the south-central part of Wyoming (Abernethy et al., 2013). They ranked fifth of seven species (five of 112 individuals) captured in late summer-early autumn 2010–2011 by mist netting over water at elevations ranging from 1,568 to 3,116 meters in lodgepole pine, Engelmann spruce, subalpine fir, and Rocky Mountain juniper forests with open sagebrush and grassland habitats on the northern range of Yellowstone National Park, northwestern Wyoming (Johnson et al., 2017).

South Dakota**:** Turner (1974) referred to long-legged myotis as the most common and widely distributed bat of the genus throughout the Black Hills in South Dakota and Wyoming. They were the second-most common species of bat (259 captures among 1,197 individuals of seven species) and the most common species of *Myotis* captured during summer 1995–1997 in the ponderosa pine dominated Black Hills of South Dakota at elevations ranging from 1,000 to 1,910 meters (Cryan et al., 2000), and the most abundant bat (47 of 209 individuals of nine species) captured over water sources near Jewel Cave National Monument, South Dakota, where males were predominant (Choate and Anderson, 1997). This species was much less common (sixth in abundance, with 13 bats among 405 individuals of nine species) at the lower elevations (less than 1,000 meters) of Badlands National Park in western South Dakota (Bogan et al., 1996).

Elevational Differences in Habitats among Sex and Age Classes: In topographically diverse areas, some species of bats are segregated in distribution by sex and age. Early mammalogists have noted that whereas males may use higher elevations, females of several species of western bats tend to use lower elevations to form maternity colonies (for example, Howell, 1920a). Reproductive females and young form maternity colonies at lower elevations where warmer temperatures promote rapid growth and development of young, whereas males and non-reproductive females favor cooler higher elevations where deeper daily torpor can be achieved (see review in Weller et al., 2009). In ponderosa pine forests of the southern Black Hills in South Dakota, reproductive female long-legged bats were more likely to be captured in mist nets over water at lower elevations than males and non-reproductive females (Cryan, 1997; Cryan et al., 2000). In ponderosa pine and piñon-juniper woodlands of the Cibola National Forest in New Mexico, a significant effect of elevation on probability of capturing reproductive females versus non-reproductive females and males was not detected, although a much higher proportion of reproductive females was found in the piñon-juniper dominated Gallinas Mountains (elevation 2,133 to 2,573 meters) than in the ponderosa-pine dominated San Mateo Mountains (elevation 2,347 to 2,682 m; Chung MacCoubrey, 2005). Females outnumbered males at Mesa Verde National Park in southwestern Colorado, where capture sites over water ranged from 1,890 to 2,361 m, and the proportion of females did not vary between years (O'Shea et al., 2011a). Allen (1939) suggested that only males reached the highest elevations in California (but based on limited data).

Foraging and Dietary Analysis.— Foraging home ranges of long-legged myotis in northern Idaho did not vary among adult males and pregnant or lactating females, ranging in area from means of 304 to 647 hectares; habitats used for foraging favored stands of medium-sized trees in mid-slope positions (Johnson et al., 2007). Several radio-tagged individuals in ponderosa pine forests in northwestern Arizona foraged at least 10 kilometers away from day roosts (Herder and Jackson, 2000); they were captured at distances as far as 9.3 kilometers away from diurnal roosts in the Jemez Mountains of New Mexico (Bogan et al., 1998).

In the Huachuca Mountains of southeastern Arizona, long-legged myotis were observed to forage at dusk among the tops of oak trees (Hoffmeister and Goodpaster, 1954). They were characterized as rapid and direct flyers based on additional observations in southeastern Arizona, where they hunted flying insects (moths, beetles, and flies) at tree-top level along margins of clumps of trees, fixing on prey at distances of five to 10 meters (Fenton and Bell, 1979). In southern Alberta, Canada, light-tagged individuals were observed foraging in the open in forested areas and high along cliff walls, and the diet mainly consisted of lepidopterans (Saunders and Barclay, 1992). They were described as foraging relatively high (about 10 meters above) over forest canopy along the banks of the Okanagan River in southern British Columbia (Fenton et al., 1980).

Dietary studies suggest that lepidopterans are the dominant food group for long-legged myotis. Moths made up most of the diet in Oregon, followed by other groups, such as homopterans, coleopterans, and isopterans (Whitaker et al., 1977; Whitaker et al., 1981; Henny et al., 1982; Ober and Hayes, 2008). Dietary analysis of stomach contents of individuals from northwestern Colorado indicated that lepidopterans were the major dietary component, followed by trichopterans and coleopterans in descending order of proportional frequency, with other groups of insects each constituting less than 10% (Armstrong et al., 1994). Moths also were the dominant dietary item of these bats in a ponderosa pine forest in northern Arizona (Warner, 1985); in northern Idaho the diet was primarily lepidopterans, followed by coleopterans and to a lesser degree other groups (Johnson et al., 2007; Lacki et al., 2007). Stomach contents of eight bats from southeastern Montana contained lepidopterans, with additional items including small coleopterans, trichopterans, homopterans, dipterans, and hymenopterans (Jones et al., 1973). They were described as moth strategists and open-air foragers based on dietary analysis of bats sampled in the San Mateo Mountains of New Mexico (Black, 1974). The diet was primarily lepidopterans followed by neuropterans, trichopterans and coleopterans in descending order of proportional volume, with lesser amounts of other prey (including caterpillars) taken during a spruce budworm (*Choristoneura occidentalis*) outbreak in Douglas fir forests of southern British Columbia (Wilson and Barclay, 2006).

Long-legged myotis were in the species group sampled by Adams et al. (2003) that preferred drinking at watering places with higher concentrations of calcium and other minerals, perhaps providing a supplement to dietary intake that would be most critical to reproductive females and weaned volant juveniles.

Roosting Habits.— Winter Roosts: These bats have been observed hibernating in caves at Jewel Cave National Monument, South Dakota (counts up to 50; Choate and Anderson, 1997), Azure Cave in Montana (Hendricks et al., 2000), and at Cadomin and Wapiabi caves in Alberta (10 torpid individuals in both caves combined; Schowalter, 1980). Hibernating long-legged myotis were often not distinguished from other species during internal winter surveys at these caves.

Sixty-seven were observed at seven caves in western Washington during winter months in 1967–1971, predominantly males (58 males and nine females) and mostly solitary or as pairs (Senger et al., 1974). In Washington and Oregon, they were the most frequently encountered bat found hibernating in searches of 650 caves or mines during winters 1982–1989; none were found in mines, but 124 were found at eight caves, sometimes in clusters (Perkins et al., 1990).

Single individuals were observed hibernating in abandoned mines in the San Gabriel Mountains (Vaughan, 1954) and in the White Mountains (Szewczak et al., 1998) of California. Two hibernating males were observed in an abandoned mine tunnel in Mohave County, northwestern Arizona at about 2,025 meters elevation (Cockrum et al., 1996), and three bats were reported hibernating in a mine in northeastern Montana (Swenson and Shanks, 1979). Bridges served as winter roosts of small numbers (one to 11) of this species in the central Sierra Nevada of California (Pierson et al., 2001). Given a paucity of observations of large numbers of these bats observed hibernating in caves and mines, it is possible that in some areas this species may overwinter in less conspicuous rock crevices, as has been established for big brown bats in northern Colorado (Neubaum et al., 2006) and Alberta, Canada (Klüg-Baerwald et al., 2017), and as was postulated by Twente (1960) for some bats in Utah.

Warm Season Roosts in Buildings, Bridges, Caves, and Mines: Long-legged myotis have been found roosting in buildings and bridges, caves, abandoned mines, rock crevices, and trees and snags during warmer months. A maternity colony of about 500 bats was reported in crevices beneath the roof at old Fort Tejon on the slopes of the Tehachapi Mountains in Kern County, California (Dalquest and Ramage 1946), and up to 24 roosted colonially in buildings in the Jemez Mountains of New Mexico (Bogan et al., 1998). Bridges were found to serve as diurnal roosts of small numbers in the central Sierra Nevada of California (Pierson et al., 2001). These bats (primarily males) were found roosting in Jewel Cave in South Dakota during summer (Choate and Anderson, 1997). Males also predominated among mist-net captures at the mouth of Azure Cave at 1,361 meters elevation in Montana during September and October (Hendricks et al., 2000). Use of abandoned mines as maternity roosts by this species has been documented at elevations as high as 2,774 meters in Colorado (Navo et al., 2000) and at 2,850 meters in northern New Mexico (Davis and Barbour, 1970). Five used a cabin as a diurnal roost at about 2,900 meters elevation at Gothic, Colorado (Storz and Williams, 1996).

Warm Season Roosts in Rock Crevices: Although roosting habits of long-legged myotis have been most intensively studied in forests, these bats will also roost and form maternity colonies in rock crevices, and individuals will switch roosts between trees and rock crevices. They have been observed roosting singly in scattered sandstone outcrops in spruce-fir forests at 3,500 meters in Colorado (Storz and Williams 1996), in groups in rock outcroppings and "hoodoos" in ponderosa pine forests in northwestern Arizona and in the Jemez Mountains of New Mexico (Bogan et al., 1998; Herder and Jackson, 2000), and in a rock crevice in a Douglas fir-western hemlock forest in Oregon (Ormsbee and McComb, 1998). A maternity colony of 180 was located in a crack in an eroded stream bank in a "practically treeless" area in the badlands of western Nebraska (Quay, 1948:181). In the Black Hills of South Dakota, four of 10 radio-tracked bats roosted in nine rock crevices, including lactating females (Cryan et al., 2001). In ponderosa pine forests of the eastern Cascade Range in Washington and Oregon, about 15% of roosts found by radio tracking 87 adult females were located in 34 crevices in rock outcrops, talus slopes, or boulder fields, with 15 individuals using only rock roosts or switching between rock roosts and snags; the majority of other roosts (72 bats) were in snags (Baker and Lacki, 2006). Nineteen pregnant or lactating females were radio tagged in piñon-juniper woodland or ponderosa pine forests at Mesa Verde National Park in southwestern Colorado, with 14 of these females successfully tracked to roosts: all roosts were in rock crevices on steep slopes or in cliff faces of canyon walls at a mean elevation of 2,180 meters, with a group of 131 bats observed exiting at emergence at one roost (logistic and safety issues prevented counts at other roosts; O'Shea et al., 2011a). In western Colorado, Neubaum (2017) radio tracked six reproductive females to seven roosts, five in crevices in cliffs and two in trees.

Warm Season Roosts in Trees and Snags: Roosting habits of long-legged myotis have been studied in detail in forests of the Pacific Northwest. In Douglas fir forests of the western Oregon Cascade Mountains, Arnett and Hayes (2009) located 105 roosts of 55 radio-tracked females in conifer snags. Bats primarily used Douglas fir (but at a frequency that did not differ from that of randomly available snags), with western hemlock and western red cedar snags used at a much lower frequency. Snags used as roosts were in stands that were mostly greater than 40 years old (Arnett and Hayes, 2009). Individuals used one to eight unique roosts (mean 2.8 ± 0.2 SE roosts) during one to 18 days of radio tracking (mean 8.4 ± 0.6 SE days), switching roosts up to eight times (mean 2.5 ± 0.3 SE switches) during tracking periods. Use of snags was higher as tree girth increased, and as the number of smaller snags nearby increased (Arnett and Hayes, 2009). The roosting habits of this species also were studied in the central Oregon Cascades (Ormsbee, 1996; Ormsbee and McComb, 1998). Radio-tagged bats were tracked to 41 roosts: 36 in snags, four in live trees, and one in a rock crevice. Snags used as roosts ranged from 33 to 44 meters in height (95% CI) and 83–110 centimeters in diameter (95% CI), with 72% in Douglas fir snags and the remainder in western hemlock or western red cedar snags (Ormsbee and McComb, 1998). Snags used as roosts were generally higher than the surrounding canopy and were more often found in uplands rather than riparian habitats, although roost snags were closer to streams than randomly selected locations (Ormsbee and McComb, 1998). Bats followed in this study switched roosts about every two days but tended to roost in groups of trees within a discrete area (Ormsbee, 1996). The largest maternity group observed was over 300 bats in a fire-hollowed western red cedar; fire hollows are rare and have different microclimates than cracks in snags (Ormsbee, 1996; Ormsbee and McComb, 1998).

In ponderosa pine-dominated forests of the eastern Cascades of Oregon and Washington, Baker and Lacki (2006) radio tracked 87 adult females and located 229 roosts (195 snags and 34 in rock crevices). Bats were tracked for an average of 9.7 ± 1.1 SE days (range 1–24) and used up to 10 unique roosts, averaging 3.6 ± 0.3 SE roosts during each tracking period, and switching roosts every 2.7 ± 0.2 days (range one to 20; Baker and Lacki, 2006). Distances between successive roosts averaged 1.4 ± 0.1 SE kilometers. About half of the roosts in snags were in ponderosa pine, with most of the remaining snags in grand fir (*Abies grandis*) and white fir (*A. concolor*). Nearly all roosts in snags were under exfoliating bark. Thermal regimes under exfoliating bark at roosts used by long-legged myotis in these two species of trees as measured in Oregon and Idaho were warmer than ambient at night; temperatures under bark are more stable than ambient air, favoring torpor in the coolness of morning with passive re-warming later in the afternoon (Lacki et al., 2013). About half of the roosts were of solitary individuals, a third housed two to 49 bats, and the remainder from 50 to 459 bats (Baker and Lacki, 2006). Group sizes were smaller prior to parturition. Lactating and postlactating females favored snag roosts that were located more upslope and had thicker exfoliating bark, perhaps because thicker bark may confer greater thermal stability for developing young (Baker and Lacki, 2006). Larger colonies used snags that were larger in diameter (a general preference for larger snags was also found by Johnson et al., 2007 in Idaho) and taller than snags used by small groups and individuals; all snags used as roosts were larger, taller, and had more remaining bark than randomly sampled snags. Snag roosts were found in areas with high densities of other large snags (Baker and Lacki, 2006). Attrition of snags used as roosts was 22.7% over a single year in the eastern Cascades study (Baker and Lacki, 2006).

A subsequent study investigated snag use by long-legged myotis at roost (microscale), stand and landscape (mesoscale), and landscape (megascale) levels in forests consisting of ponderosa pine and other species in Washington, Oregon, and Idaho (Lacki et al., 2010). A total of 153 adult females were radio tracked to 395 roosts on six watersheds and roost use was compared with randomly selected roosts that were verified as lacking use by bats. The importance of different scales in influencing roost use varied by region. In Washington and Oregon, the amount of surface area of a snag that was covered with exfoliating bark provided the best model for explaining roost site selection by females (with greater amounts favored), whereas in Idaho measurements of the degree of fragmentation and foraging habitat quality provided the highest-ranking model (Lacki et al., 2010). The most important characteristics in Washington and Idaho were amount of exfoliating bark on the snag, the height of the snag, and whether the top was broken (intact tops favored); no stand-landscape or landscape level characteristics had high importance values. In Idaho, roost scale characteristics had low importance values, but four characteristics were important at the higher levels: live tree density, stand size, amount of edge within 750 meters (less favored), and number of forested stands within 750 meters (fewer favored; Lacki et al., 2010). Proximity of roosts to water or variables indicating greater ease of roost-switching were not important in this study, but characteristics that indicated greater forest fragmentation had more negative associations with roost use. This study emphasized the regional differences that can occur among factors of importance to roosting bats (Lacki et al., 2010).

Over the longer term, Lacki et al. (2012) followed fates of 339 snag roosts used by long-legged myotis in Washington, Oregon, and Idaho. Half-lives of snags were less than three years after discovery. Snag persistence varied with region and species of tree (fir snags were least persistent), and snags that were shorter in height, larger in diameter, and had fewer remaining branches were likely to persist the longest (Lacki et al., 2012).

Vonhof and Barclay (1996) followed two radio-tagged individuals (male and female) in mixed forests of southern British Columbia, and they found that roosts were switched an average of 11 days for the female and five days for the male, with distances between roost trees averaging 28 meters in two moves of the female, and 206 meters in one move of the male. These five roosts were all under loose bark of unspecified species of conifers (Vonhof and Barclay, 1996). This species has been found roosting in cavities in both conifers and deciduous trees in central British Columbia (Psyllakis and Brigham, 2006) and under bark of a ponderosa pine in southeastern Montana (Jones et al., 1973).

In Yosemite National Park in the California Sierra Nevada mountain range, two male radio-tagged long-legged myotis were discovered roosting during summer in basal hollows of giant sequoia trees, under bark in snags of sugar pine, and in a ponderosa pine snag (Pierson et al., 2006). They roosted in basal hollows of legacy trees (large old trees that have been spared during harvest or other disturbances) in commercial redwood forests of northern California, where they were the species most frequently identified by DNA analysis of fecal pellets collected from these hollows (Mazurek and Zielinski, 2004; Zielinski et al., 2007).

Roosting habits of this species also have been studied in forests of the interior western states. In northern Arizona, warm season roosts of 13 radio-tracked adult females were all located in ponderosa pine snags (Rabe et al., 1998a). In a ponderosa pine forest undergoing extensive management for restoration of historic characteristics on Mount Trumbull in northwestern Arizona, this species roosted primarily in ponderosa pine snags and switched roosts every one to five days (Herder and Jackson, 2000). Utilized snags were taller and larger in diameter, were on lower slopes, and had more exfoliating bark than randomly selected snags. Roost snags were also located closer to drainages and forest openings, had less dense canopy cover, were in stands with larger trees, and more often were in restoration areas than were randomly selected snags (Herder and Jackson, 2000). Long-legged myotis females (*n* = 27) radio tracked in east-central Arizona ponderosa pine forest roosted in 26 snags (18 in ponderosa pine and 8 in snags of other species), one live Gambel oak and a single live Douglas fir, with mean colony sizes of 56 bats observed in exit counts (range up to 125; Saunders, 2015).

Bats in ponderosa pine forests of the Black Hills of South Dakota roosted in ponderosa pine snags that were greater in diameter but did not differ in height compared to randomly selected snags; tree spacing and numbers of snags were greater in roost plots than in randomly selected plots, and more roosts were on south-facing slopes than expected (Cryan et al., 2001). Ten bats tracked two to 14 days used 16 roosts (seven in tree snags), averaging 3.4 days per roost with exit counts ranging one to 31 bats (Cryan et al., 2001).

In piñon-juniper woodlands of the Gallinas Mountains of New Mexico, Chung-MacCoubrey (1996) found maternity colonies numbering 67–200 individuals roosting in ponderosa pine snags or live ponderosa pines with long, vertical cracks and loose bark. These trees were in isolated stands or “stringers” along arroyos and at the piñon-juniper woodland-ponderosa pine forest ecotone. Lactating females in mid- to late summer did not roost in colonies but changed roosts daily, moving among snags and roosting under sloughing bark. Year-to-year reuse of roosts in trees was documented (Chung-MacCoubrey, 2003). A colony of over 33 bats was found roosting under bark of a fir tree in the mountains of Jalisco, Mexico (Baker and Phillips. 1965).

Night Roosts: Long-legged myotis use night roosts after feeding, as has been documented at several mines and caves in the Black Hills of South Dakota (Turner, 1974), at bridges and buildings in California (Dalquest and Ramage, 1946; Dalquest, 1947a; Pierson et al., 1996b, 2001), at bridges and caves in Oregon (Albright, 1959; Perlmeter, 1996; Ormsbee and McComb, 1998), and at abandoned mines in Colorado (Storz and Williams, 1996; Navo et al., 2002). Night roosting at bridges in Oregon primarily involved females gathered in clusters (males tended to roost solitarily) for energetic advantages, particularly during late pregnancy; night roosts were typically warmer than ambient air (Perlmeter, 1996).

POPULATION ECOLOGY.— **Litter Size, Natality, and Female Reproduction:** Mating occurs in early autumn, with some first-year males apparently capable of breeding and engaging in swarming behavior observed at entrances to caves used as hibernacula (Druecker, 1972; Schowalter, 1980). Not all females are likely to reproduce in their first year of life (Druecker, 1972), but estimates of proportions of one-year-olds that are non-reproductive are unavailable. Birth occurs once annually in late spring or early summer. Litter size is one, based on preparation of 101 specimens in California (Dalquest and Ramage, 1946) and microscopic examination of reproductive tracts in New Mexico (Druecker, 1972). Single fetuses also were found in 14 females from Nevada (Hall, 1946), five females from Arizona (Cockrum, 1955; Cockrum and Ordway, 1959), three females from Colorado and five females from Wyoming (Findley, 1954), five females from western South Dakota (Jones and Genoways, 1967; Andersen and Jones, 1971; Turner, 1974), three females from mountains of southern Nevada and southern California (Grinnell and Swarth, 1913; Vaughan, 1954; Deacon et al., 1964), two females from southeastern Montana (Jones et al., 1973), two females taken in Jalisco, Mexico (Watkins et al., 1972), and a female from Baja California, Mexico (Jones et al., 1965).

The proportion of breeding females varies with place of capture (higher at maternity colonies) and ecological conditions such as drought or habitat and elevation. Dalquest and Ramage (1946:62) noted pregnancy in all of 20 females sampled on 2 June 1945 and “almost all” of 81 females sampled on June 4, 1945 at the maternity roost at old Fort Tejon on the slopes of the Tehachapi Mountains in Kern County, California. Natality of adult females captured at watering places at Mesa

Verde National Park in southwestern Colorado during summer varied with the amount of spring precipitation, averaging 27% in 180 females during a drought year and 68% in 122 females the following year when spring precipitation and insect abundance were higher (O'Shea et al., 2011a; Snider, 2009). An earlier study at Mesa Verde National Park during 1989–1994 reported that at least 16 of 40 (40%) adult females taken over water were pregnant or lactating (Chung-MacCoubrey and Bogan, 2003). None of 64 adult females captured in subalpine habitats at 2,900 to 3,500 meters in Colorado during 1993 and 1994 appeared reproductive (Storz and Williams, 1996), but non-reproductive females may select higher elevations than reproducing females (see above). In ponderosa pine forests of the eastern Cascades in Washington and Oregon, Baker and Lacki (2006) reported that 74% of 87 adult females captured over water were reproductive. Findley (1954) reported that all of 5 females taken near Jackson Hole, Wyoming were pregnant.

In the Jemez Mountains of New Mexico, the proportion of adult females captured that were reproductive varied from 17% (*n* = 12) in a drought year to 52% (*n* = 25) in a year with more normal precipitation (Bogan et al., 1998), whereas in the Mogollon Mountains of southwestern New Mexico and adjacent Arizona 65 of 106 females (61%) captured primarily over water during June and July in 1958 to 1963 were reproductive (C. Jones, 1964). Long-legged myotis (*n* = 249) captured at a maternity colony at 2,850 meters in northern New Mexico during 1968, in contrast, were "nearly all" pregnant (Davis and Barbour, 1970:263). In ponderosa pine forests of northern Arizona, 55 of 182 females (30%) sampled over water were reproductive in 1993–1995 (Morrell et al., 1999), and apparently five of 18 (28%) taken in June and early July in the Chiricahua Mountains of southeastern Arizona were reproductive (Cockrum and Ordway, 1959). Seven of 13 females (54%) taken in July in southeastern Montana were reproductive (Jones et al., 1973). Turner (1974) reported only one reproductive female among 18 (6%) examined in the Black Hills region of South Dakota, whereas Cryan (1997) reported that 14 of 23 females (61%) captured over water in the Black Hills during 1989–1996 were pregnant. Three of six females taken from late June to early August in northwestern South Dakota were reproductive (Andersen and Jones, 1971). None of four adult females captured during summer in west-central Nevada were reproductive (Kuenzi et al., 1999), whereas one of five (20%) taken over water in Clark Canyon during June was reproductive (Deacon et al., 1964). The proportion reproductive for the cumulative total females taken at locations away from maternity roosts over all U.S. locations and years was 42% (383 of 910 bats).

Survival: We are unaware of any published literature with quantitative data on survival for this species. The maximum longevity reported for the long-legged myotis is 21 years (Tuttle and Stevenson, 1982).

Mortality Factors: Mortality factors potentially influencing long-legged myotis populations are poorly known. Mortality from rabies occurs in this species (for example, Constantine, 1979; Mondul et al., 2003; O'Shea et al., 2011b), but a high prevalence of rabies-virus-neutralizing antibodies in bats sampled in Colorado (Bowen et al., 2013) suggests some degree of immune resistance to this virus. Twenty-four were found dead from rabies during September 2007 in Lane County, Oregon (U.S. Geological Survey, 2015). The presence of alpha-coronavirus RNA was detected in 8% of a sample of 147 seemingly healthy individuals netted over water in Colorado, with detections made in three consecutive years at one sampling area (indicating likely persistence of infections within the population), but the significance of these viruses as possible mortality factors remains unknown (Osborne et al., 2011). Similarly, helminth, coccidial protozoan, and ectoparasite infections have been detected in this species, but impact of these infections on mortality (if any) has not been determined (Whitaker and Wilson, 1974; Rausch 1975; Duszynski et al., 1999; Ritzi et al., 2001; Seville and Gruver, 2004). About 50 emaciated individuals were found dead from otherwise unknown causes in Lewis and Clark County, Montana (U.S. Geological Survey, 2015).

Although relatively abundant in nearby forests, no long-legged myotis were recovered in searches for carcasses at a neighboring wind power facility in southern Wyoming (Gruver, 2002). One was found dead at a wind-generating facility in Alberta, Canada (Baerwald and Barclay, 2011). White-nose syndrome has not been reported for this species. Hamm et al. (2017) discovered actinobacteria (including *Streptomyces*) with anti-fungal properties on wings of these bats and postulated that actinobacteria may have defensive properties against the fungus that causes white-nose syndrome as it moves into western North America.

Direct mortality due to environmental contaminants also has not been documented for this species. Concentrations of DDE and other organochlorines in long-legged myotis collected in Oregon in the 1970's following a large-scale forest spraying with DDT were higher than in other species of bats sampled in the study area, but not at concentrations indicative of mortality (Henny et al., 1982). Monitoring for metals and radiation is planned for individuals sampled at a uranium mine site in Arizona (Hinck et al., 2014).

Population Trend: Geluso and Geluso (2012) reported no apparent declines in numbers of long-legged myotis captured intermittently over a 34-year period at a pond in the San Mateo Mountains of New Mexico, after adjusting captures for variation in precipitation. Ellison et al. (2003) compiled a database of 290 observations of colony sizes at 186 locations in 13 western states. Four annual counts each spanning four- to 21-year periods from one summer colony and two hibernating colonies in caves in South Dakota and Washington were analyzed for trends, but none were detected (Ellison and other, 2003).

Weller (2008) evaluated sampling design considerations for use of occupancy estimation models to assess population status and habitat associations of long-legged myotis in the Pacific Northwest. Occupancy was determined using both captures in mist nets and echolocation recordings during four surveys at 51 carefully selected sites in Washington, Oregon, and northern California. Occupancy was estimated based on a series of habitat models (including successional stage and conservation reserve categories) that were ranked using Akaike's Information Criteria. They were detected at 32 sites (observed occupancy of 0.627). Model-averaged detection probability estimates were 0.358 ± 0.06 (SE) and overall occupancy estimates were 0.754 ± 0.13 (SE) using the best ranking model. Point estimates of occupancy were higher in late succession/old growth habitat (Weller, 2008).

Species dynamic distribution models were constructed using Bayesian hierarchical modeling techniques for 12 species of bats in Washington and Oregon based on an eight-year monitoring program; bat activity was sampled with mist nets and acoustic detectors, and the analysis accounted for detectability and annual turnover in bat occurrence (Rodhouse et al., 2015). This species did not show a decline in occurrence probabilities with time (Rodhouse et al., 2015).

MANAGEMENT PRACTICES AND CONCERNS.— Given the fair amount of research completed on forest use by this species, long-legged myotis have been recommended as a focal species for measuring the effects of habitat manipulation prescriptions on snag density in the Pacific Northwest (Kroll et al., 2012). Forest management that provides tall, large-diameter snags exposed to sun would favor this species in the Oregon Cascades (Ormsbee and McComb, 1998). In studies of roosts of several species of bats including this species in Douglas fir forests of Oregon and Washington, Arnett and Hayes (2009) recommended retention of all large snags that protrude above the canopy, have limited canopy closure, or are located near edges of gaps or stands. They also recommended maintaining patches of snags in older (greater than 40 years) stands, particularly in upland rather than riparian areas (Arnett and Hayes, 2009).

Because of the short half-lives (less than three years after discovery) of typical snags used by long-legged myotis in the drier forests of the eastern Cascades of Washington and Oregon and the Rocky Mountains in Idaho, Lacki et al. (2012) recommended that forest management be designed to regularly replenish snags suitable as roosts following rotation harvests (for characteristics of snags used as roosts see above under "**Roosting Habits**"). The half-lives of snags used as roosts were found to typically be much shorter than those of snags that were not specifically known to be used as roosts (Lacki et al., 2012).

Frequent roost switching and the relatively short lives of exfoliating bark roosts indicate that long-legged myotis and other species utilizing ponderosa pine snags with exfoliating bark may require more suitable snags than are needed by cavity-nesting forest birds (Rabe et al., 1998a; Baker and Lacki, 2006). Baker and Lacki (2006) suggested that snag retention for bat roosts should be large diameter (for example, greater than 60 centimeters diameter at breast height) and surrounded by snag densities of 40 snags or more per hectare in their ponderosa pine study areas in Oregon and Washington, and that both upslope (favored by lactating females) and riparian (favored by pregnant females) habitats include snags retained for bat roosting habitat. In studies of several species of bats (including long-legged myotis) roosting under loose bark or in lightning-caused cracks of snags in northern Arizona, Rabe et al. (1998a) recommended measures to help recruit ponderosa pine snags with loose bark as bat roosts. They suggested that forest management should retain large trees that die in place, thin stands of small trees to allow faster development of larger trees, and kill live large trees in areas of low snag density to hasten roost development. Prescribed fire but with protection of existing snags also may help promote development of future snags (Rabe et al., 1998a). Baker and Lacki (2006) agreed with these recommendations.

Basal hollows of "legacy trees' (large old trees that have been spared during harvest or other disturbances) are also used as roosts in redwood forests of northern California, where Mazurek and Zielinski (2004) recommended the management strategy of maintaining and recruiting such trees.

Long-legged myotis will use artificial roosts constructed to mimic exfoliating bark on snags in ponderosa pine forests in northern Arizona (Mering and Chambers, 2012). They have accepted installation of gates at the hibernaculum at Jewel Cave National Monument in South Dakota (Choate and Anderson, 1997), are reported to accept well-designed gates at abandoned mines in Colorado (Navo et al., 2000), and were captured entering gated mines in Idaho (Derusseau and Huntly, 2012).

Myotis yumanensis — Yuma myotis (Family Vespertilionidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2011b, 2015b, 2017): Sensitive Species (California, Idaho, Nevada state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Species Rounded Global Ranking G5 - Secure; Subspecies *M. y. oxalis* Rounded Global Status T2, Imperiled.

State Designations: Arizona Game and Fish Department (2012): Tier 1B Species of Greatest Conservation Need. California Department of Fish and Wildlife (2017): Special Animals List. Montana Fish, Wildlife and Parks (2015a): Potential Species of Concern. Texas Parks and Wildlife (2012): Species of Greatest Conservation Need. Utah Division of Wildlife Resources (2015; Sutter et al., 2005): Species of Greatest Conservation Need Tier III. Wyoming Game and Fish Department (2017a,b): Species of Greatest Conservation Need, Tier III.

Description.— This is a small-to-medium sized myotis. Yuma myotis (Fig. 37) show clinal geographic variation in size, with larger specimens in the northeastern part of the distribution and smaller in the southwest (Harris, 1974). In some areas where ranges overlap, the Yuma myotis may be difficult to distinguish from little brown myotis (*M. lucifugus*; Parkinson, 1979; see below). Such areas include northern California and south-central Oregon, Washington, and southern British

Columbia, and may represent zones where contact since the last glaciation has been relatively recent (Herd and Fenton, 1983). In most places where the ranges overlap, external characters that aid in discrimination between little brown myotis and Yuma myotis include darker ears, more gently sloping forehead profile, and longer dorsal hairs with glossy, burnished tips in little brown myotis (Harris, 1974; Parkinson, 1979).

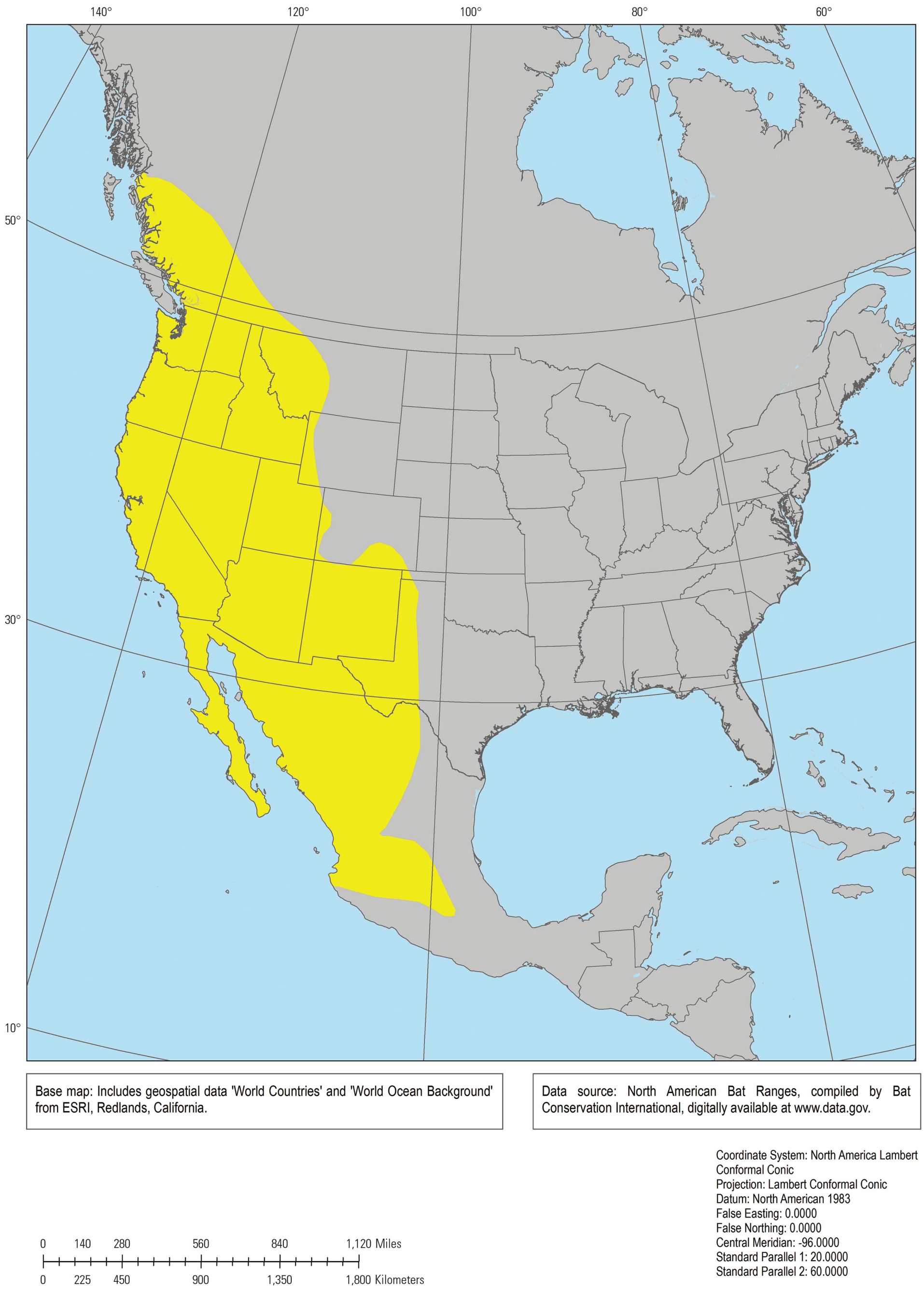
FIGURE 37. Yuma myotis, *Myotis yumanensis* (photo by J. Scott Altenbach).

Yuma myotis (Fig. 37) are more easily distinguished from other species in the genus (especially in the southwestern U.S.) by small size, no keel on the calcar, no dense fringe of hairs on the trailing edge of the tail membrane, small ears (less than 16 millimeters) that extend less than two millimeters beyond the snout when laid forward, large feet (eight to 11 mm), and small forearm length (32–38 millimeters; Hoffmeister, 1986; Schmidly, 1991; Weller et al., 2007; Braun et al., 2015). Autumn weights (when maximum fat deposition occurs) ranged from 4.8 to 7.8 grams in New Mexico (Ewing et al., 1970). Darkness of coloration is variable between and within locations (Allen, 1919; Dalquest, 1947b).

Problems that have arisen in field identification of Yuma myotis and little brown myotis in the Pacific Northwest have led to suggestions that identification can be enhanced by incorporating echolocation characteristics in addition to morphological traits, with Yuma myotis usually showing smaller forearm lengths and higher characteristic frequencies of echolocation calls (Weller et al., 2007; Rodhouse et al., 2008; but see also Carraway, 2009 and Rodhouse et al., 2009). However, in cases where 100% certainty is required in this region, a genetic analysis of each individual may be needed (Weller et al., 2007). Genetic characterizations are available for the two species in the Pacific Northwest (Zinck et al., 2004; Scott, 2005; Weller et al., 2007).

DISTRIBUTION AND SYSTEMATICS.— In the United States, the Yuma myotis is found from western Texas, the western Oklahoma panhandle, parts of southeastern Colorado, western Wyoming, and Montana west to the Pacific Ocean with major gaps in areas such as the Great Basin and higher elevations in the Rocky Mountains (Fig. 38; Harris, 1999; Braun et al., 2015). The species name has been in use since first designated in the late 1800s (Miller, 1897). Six subspecies have been named (four subspecies occur in the U.S. with distributions given by Braun et al., 2015), based partly on geographic variation in pelage coloration (Dalquest, 1947b; Harris, 1974, 1999; Braun et al., 2015). Validity of these subspecies designations has not been investigated with modern genetic approaches. Earlier morphological studies suggested the possibility that hybrids between Yuma myotis and little brown myotis may occur in those areas of overlap where it is difficult to distinguish between them. However, in British Columbia results of protein electrophoresis show no evidence of interbreeding (Herd and Fenton, 1983), nor does mitochondrial DNA analysis of specimens from Washington and Oregon (Zinck et al., 2004). A summary of other genetic findings and hypotheses pertaining to relationships of Yuma myotis with other species of *Myotis* are available in the account by Braun et al. (2015), as is a complete taxonomic synonymy of past scientific names.

The species name is geographically based, after Fort Yuma, California, the site where the type



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 38. Approximate distribution of the Yuma myotis, *Myotis yumanensis*. Species range is shown in yellow, but may not include much of the Great Basin in Utah and Nevada (see text, Braun et al., 2015).

specimen was collected (Allen, 1864). Other English common names include Fort Yuma bat, Yuma bat, Gila bat, Tejon bat, and dusky bat.

HABITATS AND RELATIVE ABUNDANCE.— Yuma myotis are often found in lowland habitats near water, and are well known to forage along rivers, creeks, ponds and irrigation canals, usually close to the water surface (for example, Dalquest, 1947b; Jones and Suttkus, 1972; Hoffmeister, 1986; Schmidly, 1991). This propensity to forage over and near water sources may bias relative abundance surveys based on captures in mist nets set over water. They also can be found in a variety of habitat types other than lowland regions, including suburban areas (Evelyn et al., 2004), and over a wide range of elevations. Specimens have been taken as high as 3,353 meters on Mount Whitney in California (Allen, 1919).

Pacific Northwest and Northern Rocky Mountains: *Oregon, Washington, and British Columbia*: Yuma myotis were described as “exceedingly scarce” in eastern Oregon (Whitaker et al., 1981:282). They ranked sixth in relative abundance (three captured among 412 individuals) out of eight species of night-roosting bats captured at five bridges in western hemlock forest in the Willamette National Forest of Oregon (Perlmeter, 1996). This species ranked eighth in relative abundance (18 among 1,057 individuals of 11 species) of bats captured over water in the predominantly ponderosa pine forests of the eastern Cascade Mountains of south-central Washington (Baker and Lacki, 2004). They were of higher relative abundance in surveys over streams and ponds in Douglas fir-western hemlock forests across the western Cascades in southern Washington and the Oregon Coast Range, ranking fourth among 12 species (18 bats out of 241 individuals; Thomas, 1988). They were the most abundant (477 individuals) of 12 species captured over water in the semi-arid Okanagan Valley of southern British Columbia, where 958 bats were captured (Woodsworth, 1981). They were also the most common species (150 captures) in the same region during an earlier study where 351 bats of nine species were taken in nets or traps over or near water (Fenton et al., 1980).

***Idaho and Montana*:** Yuma myotis were not captured in forests of multiple types in northern Idaho, where 187 individuals of eight species were taken (Lacki et al., 2007). In Montana, this species was reported to be widely distributed only in the western part of the state (Hoffmann et al., 1969).

California and Nevada: Yuma myotis appear to be high in relative abundance in surveys completed in California. This was the most abundant species taken in mist nets set over water in montane hardwood/conifer habitats along the upper Sacramento River in northern California (Siskiyou and Shasta counties), with 654 captured among 1,398 individuals of 15 species documented during 1991–1995 (Pierson et al., 1996b). They were also the highest in relative abundance at night roosts at bridges in this study area, where 1,919 were captured in comparison with 2,132 individuals of nine other species (Pierson et al., 1996b). A survey based on mist netting over water in old growth redwood forest in the Coast Range of northern California found them highest in relative abundance, with 64 captured among 142 bats of seven species (Zielinski and Gellman, 1999). Similarly, they were the highest ranking species in relative abundance (112 bats captured among 403 bats of 10 species) in mist-netting surveys in Whiskeytown National Recreation Area in Shasta County, California, where 47 sites between 256 and 1,899 meters elevation were sampled in a variety of habitats, ranging from chaparral to Douglas fir forests; habitat analyses suggested that proximity to lakes and ponds was the most important variable associated with presence of this species (Duff and Morrell, 2007).

In the wine-growing regions of Napa and Sonoma counties of northern California, echolocation activity of this species was high compared to most others, particularly in habitats with remnant vegetation (riparian forest, oak woodland, eucalypt groves) around vineyards rather than in the vineyard interiors (Kelly et al., 2016). Echolocation activity of Yuma myotis was the second highest among four species of bats detected using 22 parks in highly urban areas of San Francisco, California, constituting about 15% of total bat passes (Krauel and LeBuhn, 2016). Activity was detected in seven parks and was higher in areas closer to water and with lower proportions of native vegetation (parks characterized by non-native plantings, such as *Eucalyptus* sp.; Krauel and LeBuhn, 2016).

Yuma myotis were the most abundant species of bat (102 individuals among 390 bats of 17 species) captured in mist nets at 19 sites in the Sierra Nevada mountain range of California during 1993–1999 (Pierson et al., 2001). They ranked third most common (46 captures among 284 individuals of ten species) in a mist-net survey both over water and within forests (concentrating on groves of giant sequoia trees, *Sequoiadendron giganteum*) in Yosemite National Park in the California Sierra Nevada Range, where the preponderance of captures was over water (Pierson et al., 2006). They ranked tenth in relative abundance (24 of about 2,000 bats) among 13 species captured foraging in four vegetation zones (ranging from desert scrub to bristlecone-limber pine forests) in the White and Inyo Mountains of California and Nevada and were only taken in the Inyo Mountains on the California parts of these ranges (Szewczak et al., 1998). Most of the captures were primarily lactating females netted over small ponds in open, desert scrub habitat at 1,080 meters elevation; these bats were also observed foraging over pools at the margins of Owens Dry Lake in Inyo County, California (Szewczak et al., 1998).

In Nevada, the Yuma myotis is uncommonly reported. Hall (1946) and Miller and Allen (1928) reported these bats only from Douglas and Washoe counties in northwestern Nevada, with a single specimen from along the Colorado River on the southern border of the state. One was captured among 1,345 bats of 13 species documented in mist nets set over very small watering sources in multiple habitats (but mainly desert scrub) at the Desert National Wildlife Refuge in Clark County, southern Nevada (O'Farrell and Bradley, 1970; O'Shea et al., 2016b). This species was not captured at the Nevada Test Site (among over 2,000 bats of 13 species netted over water), where habitats were described as Great Basin and Mojave Desert scrub (Hall, 2000). They also were not captured in eastern Nevada, where 12 other species and 578 individuals were documented by mist netting over water and captures at abandoned mines and tunnels in six habitat zones (Ports and Bradley, 1996). They were not among 299 bats of 11 species captured during mist-netting surveys over water in west-central Nevada, where habitats were categorized in four vegetation zones (Kuenzi et al., 1999). Acoustic surveys in the Moapa Valley of southern Nevada indicated high use of riparian woodland, probably influenced in part by proximity to water; the species ranked seventh out of 14 based on the total time of acoustic detection (Williams et al., 2006).

Southwestern U.S.: ***Arizona*****:** This species was reported to be commonly observed foraging along the Colorado River through the Grand Canyon in northern Arizona but difficult to capture because of logistical problems (Ruffner et al., 1978). In Mohave County in western Arizona, they were seldom captured over small pools or ponds, ranking thirteenth in relative abundance (three captured among 3,458 individuals of 18 species) of species netted over such waters during 1959–1964 (Cockrum et al., 1996). They ranked tenth in abundance among 17 species of bats (12 captured of 1,171 total bats netted) taken over water mostly in ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998). These bats were rare in relative abundance, ranking fourteenth among 15 species netted over small ponds (ephemeral pools and stock tanks) and springs in ponderosa pine habitats at elevations of 2,260 to 2,620 meters in the Coconino National Forest in Arizona (three captures among 1,673 individuals documented; Morrell et al., 1999). On the Tonto National Forest in central Arizona, they ranked eighth in relative abundance (14 bats among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim (Lutch, 1996).

New Mexico**:** Yuma myotis occur in desert, grassland, and woodland zones in New Mexico, particularly riparian areas, from about 1,220 to 2,134 meters in elevation (Findley et al., 1975). They were uncommon (ranking eleventh of 15 species, with 13 among 1,532 individuals) in the Jemez Mountains of New Mexico at netting sites limited to small ponds that ranged from 1,835 to 2,729 meters in elevation (Bogan et al., 1998). Echolocation activity of these bats was commonly detected only in riparian and previously (20 years) intensely burned ponderosa pine habitats in the Jemez Mountains (Ellison et al., 2005). They were low to intermediate in abundance, ranking seventh among 16–17 species (20 captures out of 855 individuals) in mist netting over ponds during 1970 at Nogal Canyon, Socorro County, in habitats described as piñon-juniper, pine-oak woodlands, and mixed-conifer forest (Black, 1974). One individual was captured over a stock pond in piñon-juniper woodlands (among 1,222 bats of 10–11 species) in the Gallinas Mountains, and none were captured in ponderosa pine forests of the nearby San Mateo Mountains (among 447 bats of seven to eight species; Chung-MacCoubrey, 2005). At higher elevations in the San Mateo Mountains (ponderosa pine or mixed Douglas fir-blue spruce forests), none were captured in mist nets (among 1,390 bats of 10–11 species) during 19 years of sampling over a 34-year period at a natural pool in a canyon floor (Geluso and Geluso, 2012).

Also in northern New Mexico, one Yuma myotis (ranking least in relative abundance) was captured among 302 bats of 10–11 species netted in mostly ponderosa pine habitat at 2,600 to 2,885 meters on Mount Taylor (Geluso, 2008). In contrast, at a nearby lower elevation near running water, this species ranked third in relative abundance (22 bats captured) in a survey that documented six species and 130 individuals netted over water along the middle Rio Grande in the Bosque Del Apache National Wildlife Refuge of central New Mexico (Chung-MacCoubrey, 1999). Somewhat farther south, Jones (2016) documented bats captured during surveys of various habitats in the Greater Gila region of Catron, Grant, and Sierra Counties of New Mexico; Yuma myotis ranked sixth in abundance, with 17 captures among 282 individuals of 16–17 species (Jones, 2016; including data from unpublished reports of others). They ranked fourth in relative abundance (a total of 137) among 1,595 bats of 20 species taken in the Mogollon Mountains of western New Mexico and adjacent Arizona, where they were mostly captured at elevations below 1,829 meters (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, this species ranked tenth of 19 species (14 captures among 1,004 individuals), and were only taken in riparian hardwoods within mesquite-juniper woodlands at 1,465 meters (Jones and Suttkus, 1972). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species with 54 Yuma myotis, ranking tenth in relative abundance (Geluso, 2006, 2017).

Texas:. At Big Bend National Park in Texas, Yuma myotis were most common at lower elevations along the Rio Grande. During 1967–1971 they ranked seventh in relative abundance at Big Bend, with 384 captures among 4,807 captures of 18 species (Easterla, 1973). Subsequent surveys at Big Bend during 1996–1998 found them to rank eighth in relative abundance (46 among 1,978 captures of 17 species), with most captures concentrated over open water of the Rio Grande (Higginbotham and Ammerman, 2002). They ranked eleventh among 14 species (two out of 542 individuals) captured in mist nets at 108 locations over water in northern Chihuahuan desert habitats described as desert scrub, desert grassland, riparian, and juniper roughland at Big Bend Ranch State Park, northwest and upstream of the national park in the Trans-Pecos region of Texas; existence of roosts in the region led investigators to suggest greater abundance than indicated by capture frequency (Yancey, 1997). This species was not documented in a mist net survey where 1,329 individuals in 12 species were captured at Palo Duro Canyon State Park in the Texas Panhandle (Riedle and Matlack, 2013), somewhat beyond the edge of the known distribution (Ammerman et al., 2012a; Braun et al., 2015).

Central Rocky Mountains and Western Great Plains: *Colorado*: In Colorado, this species is only known from the western and southeastern parts of the state (Ellinwood, 1978; Armstrong et al., 2011). Yuma myotis ranked thirteenth in relative abundance (18 bats captured among 1,996 individuals of 15 species netted over water) in the piñon-juniper woodland and ponderosa pine forests of Mesa Verde National Park in southwestern Colorado, where they were mostly taken at lower elevations (O'Shea et al., 2011a). During an earlier study at Mesa Verde in 1989–1994, none were taken in mist nets (189 individuals of 11 other species were documented; Chung-MacCoubrey and Bogan, 2003). None were taken in mist nets set over stock ponds in the Uintah Basin of Moffat County in northwestern Colorado, where 546 bats of 11 other species were documented (Freeman, 1984). In far western Colorado, this species ranked second in relative abundance of 16 species (221 captures among 899 bats) at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during three summers of netting over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Yuma myotis was also regularly documented by both mist nets and acoustic surveys primarily in riparian and piñon-juniper habitats in Dinosaur National Monument near the perennial water sources of the Green and Yampa rivers (Bogan and Mollhagen, 2016; Neubaum and Navo, 2011). Yuma myotis were captured swarming at a cave in Garfield County, also in northwestern Colorado, at an elevation of 3,000 meters (Navo et al., 2002) and were netted in small numbers during summer at this and another cave at similar elevation (Siemers, 2002). None were captured along the northern Front Range in Colorado (including the adjacent urbanizing corridor), where 10 other species were documented and 2,538 individuals captured, verifying distributional limits (Adams et al., 2003; O'Shea et al., 2011b). In southeastern Colorado, the Yuma myotis accounted for six percent of 239 bats captured across two counties (Ellinwood, 1978). Capture sites for this species were generally below 1,700 meters elevation. As piñon-juniper woodlands transitioned to coniferous forest above 2,300 meters, a distinct transition from Yuma myotis to little brown myotis also occurred.

***Utah*:** Yuma myotis can be found in a range of habitats and elevations in Utah, but most known localities are from the eastern and southern parts of the state (Oliver, 2000). The few records in southwestern Utah range from creosote bush and mesquite scrub at 945 meters elevation to coniferous woodland at 1,981 meters (Stock, 1970). They ranked eleventh in relative abundance of 15 species (13 individuals among 572 bats) in the Henry Mountains of southeastern Utah, where they were netted over water at 1,335 to 2,621 meters elevation only prior to July; it was suggested that these bats may use the mountainous areas early in the warm season and then move down to low elevation watercourses later in summer (Mollhagen and Bogan, 1997). At Arch Canyon on the Colorado Plateau in southeastern Utah, they ranked sixth in abundance, with 14 bats captured among 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters (Mollhagen and Bogan, 2016). These bats ranked fourth in abundance (143 captures among 1,377 bats of 15 species) in mist-netting surveys over water (including the Green and Yampa rivers) at Dinosaur National Monument in northwestern Colorado and adjacent parts of Utah, at elevations ranging from 1,459 to 2,263 meters (Bogan and Mollhagen, 2016).

***Wyoming*:** Yuma myotis were previously not known from Wyoming (Bogan and Cryan, 2000), but recent mist-netting records (including reproductive females) have been reported for lower elevation basin and foothills habitat in the south-central part of the state; during 2012 they ranked seventh among 12 species (11 captured out of about 370 individuals) documented in this region (Abernethy et al., 2013). They were not documented in mist-netting surveys over streams and beaver ponds at higher elevations (2,133 to 2,896 meters) in and near the Medicine Bow National Forest in southern Wyoming, or in habitats encompassing lodgepole pine (*Pinus contorta*) and spruce-fir forests (Gruver, 2002).

***Oklahoma and Kansas*:** In Oklahoma, these bats have been found only in the western panhandle near the Cimarron River (Glass and Ward, 1959: Roehrs et al., 2008), where they were thought to be the most common species of *Myotis* in piñon-juniper woodlands (Dalquest et al., 1990). They are not known from Great Plains states north of Oklahoma (Braun et al., 2015) but conceivably could occur along the Cimarron River where it runs through Kansas (Sparks and Choate, 2000).

Elevational Differences in Habitats among Sex and Age Classes: At Big Bend National Park in Texas, only male Yuma myotis were taken above about 2,000 meters (Easterla, 1973). Disproportionate use of higher elevations by males also has been suggested for California (based on limited data; Allen, 1939, Dalquest, 1947b) and British Columbia (Fenton et al., 1980). In western Colorado, proportions of males and females did not noticeably vary by elevation; most captures of both sexes were at lower elevations close to permanent water sources (Neubaum, 2017).

Foraging and Dietary Analysis.— Yuma myotis are often observed flying close to the surface of water (for example, Dalquest, 1947b; Glass and Ward, 1959; Fenton et al., 1980). Individuals observed as they emerged from a California roost flew directly to the nearby Truckee River within 10 meters of the ground, skimming over tops of low trees and feeding for several minutes before drinking (Dalquest, 1947b). Hunting flights over pools were described as in a straight direction, but "with innumerable dips and swerves of from a few inches to six feet in one direction or another" (Dalquest, 1947b:241). Individuals were noted as flying within one meter of the surface of the water in southern British Columbia but favored feeding over slower stretches of flowing water, river banks, and near the canopies of trees in comparison with sympatric little brown myotis (*M. lucifugus*; Fenton et al., 1980). Quantitative observations (also in southern British Columbia) show that they spend less time foraging in areas with structurally complex vegetation, regardless of reproductive condition or age class, instead spending most of their foraging time over water, in open areas within 10 meters of the ground, and close to trees (Herd and Fenton, 1983; Brigham et al., 1992). Nonetheless, they also have been observed feeding low to the ground within dense willow thickets and other thick vegetation (Dalquest, 1947b), consistent with the maneuverability suggested by their wing morphology (Aldridge, 1986; Brigham et al., 1992). In northern California, echolocation activity of foraging bats was higher in areas of remnant vegetation (riparian forest, oak woodland, eucalypt groves) around vineyards than in the vineyard interior (Kelly et al., 2016). Distances moved both within nights and between seasons is not well understood for this species. Yuma myotis in western Colorado moved an average of one kilometer between capture sites and the first roost used after being radio tagged (Neubaum, 2017), although one pregnant female moved nearly 40 kilometers in just two nights after being fit with a radio, demonstrating that longer movements are possible.

Reported foods include small insects such as moths, but also include those with aquatic phases to the life cycle, particularly caddis flies, mayflies, and dipterans (including midges), many likely taken over water (Easterla and Whitaker, 1972; Whitaker et al., 1977; Herd and Fenton, 1983; Brigham et al., 1992). However, observations of this species foraging on swarms of ephemeral flying ants (*Pogonomyrmex* sp.) emerging along a cliff face (Vaughan, 1980) and their responses to artificial patches of prey created by black lights (Fenton and Morris, 1976) suggest that they can be opportunistic feeders. Under some conditions they can fill their stomachs within 15 minutes after dusk (Dalquest, 1947b). In riparian areas in the Oregon Coast Range, they had a varied diet of small insects, eating primarily dipterans, trichopterans, isopterans, lepidopterans, and spiders in descending order by proportional volume, but they also consumed insects in a variety of other groups including coleopterans, hemipterans, hymenopterans, and neuropterans (Ober and Hayes, 2008). In northeastern Oregon, they were reported to feed across a variety of insect groups, including lepidopterans (most abundant at 23% volume), coleopterans, trichopterans, homopterans, isopterans, and dipterans (Whitaker et al., 1981). Black (1974) observed these bats forage about three meters above water in the San Mateo Mountains of New Mexico, occasionally gleaning moths off the water surface but having a low proportion of moths or beetles in their diet. This species also has been observed regularly foraging low over large eddies and backwaters of major rivers in western Colorado, such as the Green, Yampa, and Colorado rivers (Neubaum, 2017).

Roosting Habits.— Yuma myotis will roost in mines, caves, buildings, bridges, cliff crevices, swallow nests, and other structures, typically in fairly close proximity to water (Dalquest and Ramage, 1946; Glass and Ward, 1959; Constantine, 1961a). They are known to share roosting structures with a number of other species, including Arizona myotis, cave myotis, fringed myotis, long-legged myotis, long-eared myotis, California myotis, big brown bats, pallid bats (*Antrozous pallidus*), and Brazilian free-tailed bats (for example, Dalquest, 1947a,b; Constantine, 1961a; Studier, 1968; Geluso and Mink, 2009). Sexes typically roost apart in summer, with males often found solitary and females in maternity colonies (Dalquest, 1947b).

Winter Roosts: Remarkably little information exists on the natural winter roosting habits of this widely distributed species (Boyles et al., 2006). Low numbers were observed in hibernation in lava caves near Mount St. Helens in Washington during winter months in 1967–1970 (Senger et al., 1974). Bridges were found to serve as winter roosts in the central Sierra Nevada of California (Pierson et al., 2001). A "few" were reported in winter in an abandoned mine in the Whipple Mountains of San Bernardino County, California (Brown, 2013:12). This species was captured swarming at a cave at an elevation of 3,000 meters in northwestern Colorado during September, suggesting they may hibernate in the region (Navo et al., 2002). It has been speculated that in Arizona and Texas these bats may migrate south for the winter (Hoffmeister, 1986; Schmidly, 1991). Mist netting of bats during winter months in central and southern New Mexico did not yield any bats of this species, although intermittent activity of 12 other species was detected with captures of 401 individuals (Geluso, 2007). Large numbers are known to roost in colonies under bridges (see below) in parts of the surveyed area of New Mexico during summer, but only a few were found at these same bridges during November through March (Geluso and Mink, 2009).

Warm Season Roosts in Rock Crevices, Trees, and Swallow Nests: A maternity colony of Yuma myotis was found in a sandstone cliff in a vertical southeast-facing crevice about 10 meters above ground level in Las Animas County in south-eastern Colorado (Ellinwood, 1978). Nineteen females (most were reproductive) were radio tracked to 27 roosts in western Colorado: all roosted in rock crevices in cliffs (Neubaum, 2017). Maternity colonies found in cliffs during the latter Colorado study were variable in size but ranged up to 189 or more individuals (Neubaum, 2017). Small (up to 30 individuals) colonies were observed roosting in narrow vertical crevices in limestone cliffs in the Verde Valley of central Arizona (Vaughan, 1980). Two solitary individuals each roosted in snags of cottonwood trees (*Populus fremontii*) along the Rio Grande at Bosque Del Apache National Wildlife Refuge in New Mexico (Chung-MacCoubrey, 1999), and a single bat was observed roosting under bark of a tree stump in southern British Columbia (Vonhof and Barclay, 1997).

Radio tracking of individual Yuma myotis of both sexes (colony attributes were not reported) captured in summer in a suburban area south of San Francisco Bay in California showed that diurnal roosts of these bats were in trees and to a lesser extent buildings (Evelyn et al., 2004). Trees used as roosts included both conifers (least redwood, *Sequoia semipervens*, and Douglas fir) and hardwoods (primarily valley oaks, *Quercus lobata*, coast live oak, *Quercus agrifolia*, and big leaf maple, *Acer macrophyllum*). Most (16 of 18) of the roost trees were alive. Roosts in live hardwood trees included cavities, cracks, and other features in trees with fungal infections, and dead or broken limbs and tops. Some individual bats switched roosts in trees about every 4.5 days, with a mean distance of 1.1 kilometers (range 0.1 to 2.7) between consecutive roosts (Evelyn et al., 2004). Trees used as roosts had larger diameters (mean of 1.15 m, greater than found in most studies of other species of tree-cavity roosting bats), and were taller than randomly selected and neighboring trees, with diameter appearing to be the key variable associated with roost tree selection; at the site level roost trees were closer to water and located in areas with higher forest cover than randomly selected comparison points (Evelyn et al., 2004).

Two maternity colonies of Yuma myotis numbering 60 and over 500 bats have been reported occupying basal hollows of redwood trees in northern California (Gellman and Zielinski, 1996). Cliff swallow (*Petrochelidon pyrrhonota*) nests were occupied by this species during August after the breeding season in the Verde Valley of central Arizona (Vaughan, 1980).

Warm Season Roosts in Caves and Mines: A maternity colony of "several thousand" Yuma myotis was reported in a cave near Pyramid Lake, Nevada in 1924 (Hall, 1946:135), and a maternity colony of unspecified size was observed in a shallow cave near Del Rio, Texas in 1903 (Bailey, 1905). They were captured at mouths of two caves at elevations of 2,770 and 3,014 meters (three bats at one cave, 14 at the other) in Colorado during summer, but type of use was unspecified (Siemers, 2002). Three abandoned mines were the most northerly maternity roosts (two colony sizes of 500–750 and one of 50–60) known in Idaho by Betts (1997). These roosts had higher and more constant relative humidity than unused mines, more constant temperatures, and were also less likely to be disturbed by people. Howell (1920a) reported a colony of about 600 females in May 1918 segregated at 30– and 60–meter depths in the Senator Mine on the lower Colorado River in Imperial County, California, with those bats closest to the entrance roosting singly and torpid, and those deeper in the mine active and in clusters. An abandoned mine used as a maternity roost was reported in the Moapa Valley of Nevada (Williams et al., 2006). A deep abandoned mine shaft has been used as a migratory stopover roost by these bats in New Mexico (Altenbach et al., 2000).

Use of abandoned mines by maternity colonies of Yuma myotis also has been documented recently in southwestern Arizona, southeastern California, and southern Nevada (Henry, 2002; Williams et al., 2006; Brown, 2013). One abandoned mine on Imperial National Wildlife Refuge in southwestern Arizona has housed a maternity colony ranging to over 3,000 adults since annual monitoring took place from 2001 to 2013 (Brown, 2013), but was reported to harbor about 9,000 in 1994 (Castner et al., 1995). Another abandoned mine on the California portion of the refuge held a maternity colony of about 2,000 Yuma myotis (Brown, 2013). Other colonies in abandoned mines in this region include about 1,500 individuals at one mine in the lower Colorado region of southeastern California, and the recent discovery of an abandoned mine housing a maternity colony of up to 5,500 bats on Bureau of Land Management property in San Bernardino County, California (Brown, 2013).

Warm Season Roosts in Buildings and Bridges: Buildings were the sites of most early records of Yuma myotis roosts. Dalquest (1947b) described roosts in multiple buildings in California and noted that all were near water, near trees, were dimly lit, and most provided dark crevices where bats roosted. Early records of roosts of this species included a maternity colony from abandoned buildings at old Fort Tejon, Kern County, California, in which 61 bats, all females or young, were taken in July 1904 (Grinnell, 1918). This site was known to house a large colony of these bats as early as 1891, but it was apparently unoccupied by this species by 1945 (Dalquest, 1947b). They were found roosting in a warehouse at San Simeon in San Luis Obispo County on the California coast, and a lone male was reported from a crevice in an abandoned house in Santa Clara County, California (Dalquest, 1947a).

Use of buildings by maternity colonies of Yuma myotis is widespread. The attic and belfry of a church in Wadsworth, Nevada housed a maternity colony of about 5,000 bats (Dalquest, 1947b) and a colony of about 30 occupied the gable of a barn near Sutcliffe, Nevada in 1926 (Hall, 1946). About 100 individuals roosted beneath an awning on a building in El Centro, Imperial County California during October (Howell, 1920a), a maternity colony of 1,500 was reported in a warehouse in Oxalis, California, and a maternity colony of unspecified size was found roosting between walls and the roof of the warehouse at San Simeon (Dalquest, 1947a). A building in the Trans-Pecos region of western Texas also was used as a maternity roost (Yancey, 1997), as was an old cabin near Malheur Lake, Oregon and an attic at Eagle Lake in northeastern California (Bailey, 1936). A maternity colony numbering 1,600 has been reported in an abandoned church as far north as British Columbia (Milligan, 1993; Milligan and Brigham, 1993), where they also apparently roosted in a mobile home in the same region (Fenton et al., 1980). A colony at San Antonio, New Mexico (elevation 1,392 meters), roosted in a church roof and steeple together with Arizona myotis (*M. occultus*), with a combined estimate of 1,800 bats of both species (Chung-MacCoubrey, 1999), and a maternity colony of 200 used the attic of a seminary at the higher elevation (2,042 meters) town of Montezuma, San Miguel County, New Mexico (Studier, 1968). About 2,000 females and young occupied a roost in the loft of a barn near Solano, California during summer, where high temperatures of 50ºC were reached at upper parts of the roosting area during the day (Licht and Leitner, 1967a). Extremes of heat in these roosts were evaded by behavioral thermoregulation and selection of appropriate microclimates within the roost when temperatures exceeded about 40ºC (ambient temperatures above 43.5ºC were lethal; Licht and Leitner, 1967a,b).

Yuma myotis were found roosting in diurnal colonies in narrow crevices under multiple highway bridges over the Rio Grande in southern New Mexico, including at least seven maternity colonies and nearly 14,000 individuals; roosting sites were at least 1.1 meters above ground, with most in bridges constructed of timbers (Geluso and Mink, 2009). A colony of at least 250 roosted under a small concrete bridge near the Rio Grande at Bosque Del Apache National Wildlife Refuge in New Mexico (Chung-MacCoubrey, 1999). Bridges were found to serve as both maternity and night roosts in the central Sierra Nevada of California, where some colonies roosted behind metal signs posted at the bridges, 10 of 20 inspected bridges held summer colonies, and six were used as night roosts; the largest colonies at bridges held over 1,000 individuals (Pierson et al., 2001). Structural features of bridges used by this species and roosting places beneath them have been described in detail elsewhere (Pierson et al., 1996b, 2001; Geluso and Mink, 2009). Use of a wooden bridge in the Bitterroot Valley of Montana by a maternity colony of several hundred was noted by Bailey (1936).

Transient spring and autumn colonies in crevices of the Davis Dam on the Colorado River near Bullhead City, Arizona numbered as high as 10,000 bats in 1960 (Cockrum et al., 1996). The London Bridge at Lake Havasu, Arizona houses a maternity colony of several thousand individuals, and a smaller colony roosts at Baseline Bridge over the lower Colorado River at Cibola, Arizona (Brown, 2013).

Night Roosts: Yuma myotis will night-roost in deserted buildings, as described by multiple authors (for example, Cary, 1911; Warren, 1942; Dalquest and Ramage, 1946; Dalquest, 1947a,b; Easterla, 1973; Pierson et al., 1996b; Adam and Hayes, 2000). Maximum aggregations of 250 to 450 individuals (primarily females and volant young) have been noted during summer in night roosts under two abandoned bridges over the Sacramento River in northern California, with individual bats showing fidelity to these night roosts from year-to-year (Pierson et al., 1996b). They also used bridges as night roosts in the Trans-Pecos region of western Texas (Yancey, 1997). Sixteen of 20 bridges inspected for night roosting in the central Sierra Nevada in and near Yosemite National Park were used as night roosts, mostly by Yuma myotis (Pierson et al., 2001). Albright (1959) reported this species to commonly night roost at a cave at Oregon Caves National Monument, and Brown (2013) noted they also use abandoned mines in southeastern California as night roosts. About 200–300 night roosted in buildings at the Imperial National Wildlife Refuge in southwestern Arizona (Castner et al., 1995). A road tunnel in western Colorado was used as a night roost by 50–100 adult female and juvenile Yuma myotis, where they roosted together with male Brazilian free-tailed bats (Neubaum, 2017).

Population Ecology.— Litter Size, Natality, and Female Reproduction: Litter size is usually one, although a female with three embryos has been documented (Finley et al., 1983). Dalquest (1947b) reported 63 females with one embryo each at multiple locations in California and at Wadsworth, Nevada. Single embryos were found in seven females from western Oklahoma (Glass and Ward, 1959) and in 12 females at Bosque Del Apache National Wildlife Refuge in New Mexico (Mumford, 1957; Commissaris, 1959). Hall (1946) reported 24 females each with single embryos in Nevada. One female from Imperial County, California, had a single embryo (Howell, 1920a), as did a female sampled in southern Colorado (Davis and Barbour, 1970). One female from Sinaloa, Mexico, also had a single embryo (Jones et al., 1972). Four females each with single clinging young were reported by Dalquest (1947b) at a California roost. Natal sex ratios are 1:1 (Milligan and Brigham, 1993).

Natality at maternity roosts has been suggested to be about 100% (Hall, 1946; Herd and Fenton, 1983), although Dalquest (1947b:245) noted that in California there are “a sizeable proportion of non-bearing females”. At Bosque Del Apache National Wildlife Refuge in New Mexico, all of 41 females sampled at a maternity roost were reproductive in 1953 (Mumford, 1957) and 34 of 35 (97%) were reproductive in 1957 (Commissaris, 1959). All of 16 females (100%) taken primarily at roosts in the Mogollon Mountains of southwestern New Mexico and adjacent Arizona during June and July in 1960 to 1962 were reproductive (C. Jones, 1964). Twenty-three of 25 females (92%) examined at a maternity roost in Wadsworth, Nevada, during 1945 were pregnant (Dalquest, 1947b), and 40 of 45 females (89%) examined at about eight different locations in California during 1945 or earlier were pregnant (Dalquest, 1947b). It has been suggested that this species gives birth at age one year in British Columbia, but based only on indirect evidence (Herd and Fenton, 1983). Frick et al. (2007; based on unpublished data from four colonies) noted only a 42% probability of female Yuma myotis breeding in their first year.

Although females measured at maternity roosts show high natality, somewhat fewer are reproductive when sampled away from maternity colonies. In British Columbia, female reproductive rates of Yuma myotis varied annually, with lowest rates during a summer with lengthy periods of cool, rainy weather (Grindal et al., 1992). Rates were 100% in 66 females captured over water in south-central British Columbia during 1979 (Fenton et al., 1980), about 90–95% in 89 females sampled over water in June and July during 1982 (Herd and Fenton, 1983), and about 18–30% in 68 bats sampled over water in June and July of 1990, an unusually wet summer when it was suspected that rainfall affected both thermal energetics and the ability to forage, perhaps resulting in resorption of embryos (Grindal et al., 1992). Ten of 12 (83%) shot over water in Monterey County, California were reproductive (Dalquest, 1947b). Easterla (1973) reported that 12 of 16 (86%) females captured in Big Bend National Park, Texas were reproductive during summers 1967–1971, as were six of eight (75%) females captured at net sites at Bosque del Apache National Wildlife Refuge in New Mexico during 1997 (Chung-MacCoubrey, 1999).

Survival: Annual apparent survival estimates were calculated for Yuma myotis at two roosts unaffected by a contaminant spill (see “Mortality” below) in comparison with two roosts in the spill area (Frick et al., 2007). Apparent survival of adults was unaffected in the spill area and increased from 0.72 to 0.88 at all four roosts over the period 1992 to 1995, coinciding with increasing habitat recovery from a prolonged regional drought; juvenile survival in the area not subject to the spill also increased (from 0.60 to 0.80) over the same time period but was always lower than adult survival and was lower in the area of the spill (Frick et al., 2007; see also "**Mortality Factors**" and "**Population Trend**" below). These survival estimates were in populations that showed accompanying positive growth in life-history stage-based models (Frick et al., 2007). An overall increase in survival with time ranked second to the importance of age group, whereas the effect of spill area ranked third in relative importance as a variable affecting survival (Frick et al., 2007). The time increase was attributed to the cessation of a major regional drought beginning with the second year of study; population growth rates were negative the first year after the spill and became positive thereafter, but with growth rates lower in the roosts in the spill-affected area (Frick et al., 2007). The maximum longevity record for this species is 14 years (Boutin and Willis, 1996).

Mortality Factors: A variety of incidental predators on Yuma myotis have been recorded. Bobcats were documented regularly preying on these bats at a maternity colony in a cave in Nevada (Hall, 1946). The habit of flying low to the ground and over water probably renders them susceptible to various terrestrial and aquatic predators (Dalquest, 1947b). Rabies infections in this species are well known (for example, Constantine, 1967; Mondul et al., 2003; Blanton et al., 2007; Streicker et al., 2010). Eighteen individuals from locations in Colorado were sampled for evidence of coronavirus infections but none were detected (Osborne et al., 2011). In spring of 2017, a Yuma myotis found unable to fly in King County, Washington was diagnosed with white-nose syndrome, indicating this fungal disease occurs in their population (Washington Department of Fish and Wildlife, 2017). Given that this species is known to form large colonies during the summer, it is possible these bats may aggregate in winter as well, which could facilitate the spread of white nose syndrome. Many species of ectoparasites and endoparasites of many different forms have been documented in Yuma myotis (reviewed in detail by Braun et al., 2015), but they were not implicated as causing mortality. They have been struck by motor vehicles (Dalquest, 1947b), a likely under-recognized source of mortality for bats in general (O'Shea et al., 2016a).

King et al. (2001) reported on the presence of 18 potentially toxic elements in small numbers of Yuma myotis collected at four locations in Arizona in 1998 and 1999. Only copper appeared to occur at exceptionally high levels, but the sources and toxic implications of these findings could not be determined. Annual apparent survival estimates of juvenile females were lower at two roosts near an area of the Sacramento River in California subject to a large spill of the agricultural soil fumigant metam sodium (the sodium salt of methyl dithiocarbamate) in comparison with estimates for unaffected roosts, perhaps a result of spill impacts on the emergent aquatic insect food base (Frick et al., 2007).

Population Trend: Population growth rates (λ) based on empirically derived life history stages ranged from about 1.1 to about 1.2 in a recovering population in northern California (Frick et al., 2007; see also "Survival" and "Mortality Factors" above). Sufficient data on U.S. colony sizes were unavailable for analysis of count-based population trends (Ellison et al., 2003), although a possible local extirpation of small colonies in central Arizona likely due to increased disturbance was noted by O'Shea and Vaughan (1999). Brown (2013) noted the absence of Yuma myotis from the Senator Mine in California near the lower Colorado River in 1991 and 2011, whereas Howell (1920a) reported a colony of about 600 females at this site.

Weller (2008) evaluated sampling design considerations for use of occupancy estimation models to assess population status and habitat associations of Yuma myotis in the Pacific Northwest. Occupancy was determined using both captures in mist nets and echolocation recordings during four surveys at 51 carefully selected sites in Washington, Oregon, and northern California, and estimated based on a series of habitat models (including successional stage and reserve categories) that were ranked using Akaike's Information Criteria. They were detected at 27 sites (observed occupancy of 0.529). Model-averaged detection probability estimates were 0.447 ± 0.07 (SE), and overall occupancy estimates were 0.586 ± 0.10 (SE) using the highest-ranking model. This was the lowest model-averaged occupancy estimate of eight species sampled. Point estimates of occupancy tended to be higher in reserve habitat, but greater precision and model certainty would be useful to improve all estimates (Weller, 2008).

Species dynamic distribution models were constructed using Bayesian hierarchical modeling techniques for 12 species of bats in Washington and Oregon. The analysis was based on an eight-year monitoring program; bat activity was sampled with mist nets and acoustic detectors, and the analysis accounted for detectability and annual turnover in bat occurrence (Rodhouse et al., 2015). This species did not show a decline in occurrence probabilities with time (Rodhouse et al., 2015).

Management Practices and Concerns.— Maternity colonies "are very sensitive and quickly abandoned if disturbed" (Schmidly, 1991:78). Intentional disturbances should be avoided or timed for periods when individuals are absent from roosting places. Replacement of a bridge used by a colony during the early maternity season in New Mexico likely resulted in deaths of thousands of Yuma myotis and Brazilian free-tailed bats (Geluso and Mink, 2009). Past efforts by the U.S. Army Corps of Engineers to eliminate colonies in crevices of the Davis Dam on the Colorado River near Bullhead City, Arizona were reported by Cockrum et al. (1996). To avoid disturbance by unauthorized visitors, the National Park Service has erected a large fence around abandoned mine shafts, as well as built other bat-compatible closures at Joshua Tree National Park and Lake Mead National Recreation Area to protect colonies of this species (Burghardt, 2000). An abandoned mine housing a maternity colony of 300–500 Yuma myotis on Bureau of Land Management property in southeastern California also has been successfully gated for protection of these bats, as have abandoned mines on Imperial National Wildlife Refuge lands in southern Arizona and southeastern California (Henry, 2002). However, counts at one mine on the refuge declined substantially following installation of additional cupolas and gates on upper shafts (Brown, 2013). Knowing locations of Yuma myotis maternity colonies in cliffs at Colorado National Monument has helped resource management staff there determine the need for seasonal closure of recreational climbing routes that intersect or closely approach those sites (Neubaum, 2017).

Evelyn et al. (2004) noted that size of available roosting trees could be a limiting factor in some areas if this species generally prefers roosting in especially large trees, as found in their study on the San Francisco Bay peninsula.

Yuma myotis seem strongly associated with river canyons and may be particularly vulnerable to habitat loss from large-scale water impoundments such as reservoirs. Major water development projects have the potential to not only reduce productive foraging habitat through submersion but also eliminate adjacent roost habitat in rock crevices of canyon walls.

Nyctinomops macrotis — Big free-tailed bat (Family Molossidae)

Conservation Status.— National and International Designations: U.S. Fish and Wildlife Service (1994, 1996a,b): Species of Concern (inactive, former Category 2 candidate for listing under the U.S. Endangered Species Act). Bureau of Land Management (2009a, 2010c, 2011b): Sensitive Species (Colorado, Nevada, and Utah state offices). International Union for the Conservation of Nature (2017): Least Concern. NatureServe (2017): Species Rounded Global Ranking G5, Secure.

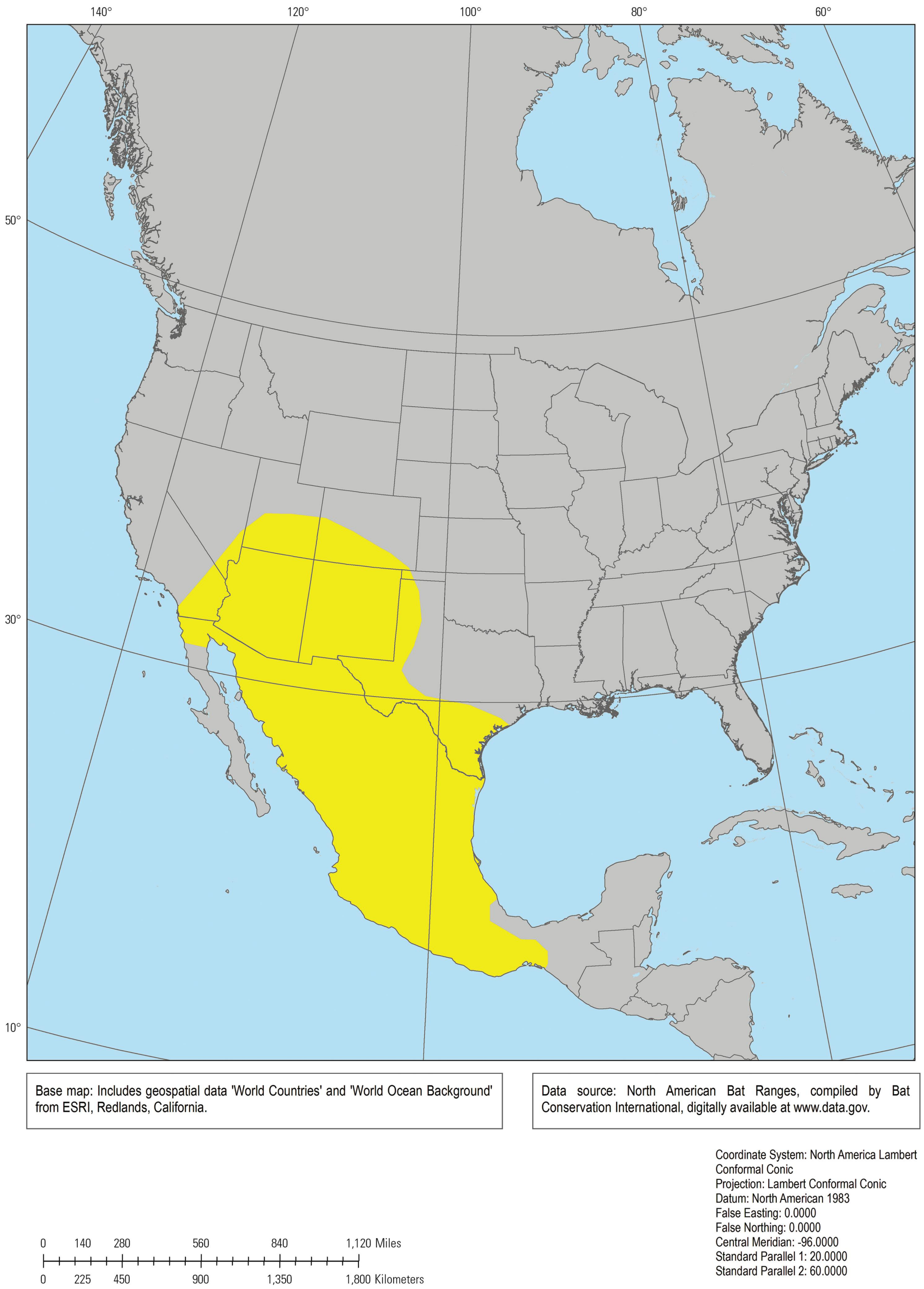
State Designations: California Department of Fish and Wildlife (2015b, 2017): Special Animals List, Species of Special Concern. Colorado Parks and Wildlife (2015b): Species of Greatest Conservation Need, Tier 2. New Mexico Department of Game and Fish, 2015: Sensitive taxa (informal). Texas Parks and Wildlife (2012): Species of Greatest Conservation Need. Utah Division of Wildlife Resources (2015, Sutter et al., 2005): Species of Greatest Conservation Need.

FIGURE 39. Big free-tailed bat, *Nyctinomops macrotis* (photo by J. Scott Altenbach).

DESCRIPTION.— The big free-tailed bat (Fig. 39) is among the larger bats found in the United States. Forearm lengths range from 58 to 64 millimeters, body mass ranges 22 to 37 g, and wingspans range to 436 millimeters (Barbour and Davis, 1969; Milner et al., 1990; Parish and Jones, 1999; Higginbotham and Ammerman, 2002). The hairs are bicolored and lighter at the base, and the pelage varies from gray to medium and darker shades of brown (Milner et al., 1990), with considerable color variation among individuals within a colony (Borell, 1939). The upper lips are wrinkled. As typical for a molossid bat, the tail extends beyond the interfemoral membrane, the ears are large, rounded airfoils joined at the midline, and the long narrow wings render these bats capable of rapid flight (Vaughan, 1966).

DISTRIBUTION AND SYSTEMATICS.— Although the species is widely distributed throughout the Americas and the Caribbean, in the United States populations seem localized and the core of the range appears to be the rugged, rocky landscapes of the Four Corners states (Fig. 40). Extralimital records are widespread in North America and include places as far from the typical range as British Columbia, Kansas, Iowa, Missouri, Oklahoma, and South Carolina (Cary, 1911; Bowles, 1975; Dalquest et al., 1990; DiSalvo et al., 1992; Nagorsen and Brigham, 1993; Pitts et al., 1996; Sparks and Choate, 2000); these may represent post-breeding wandering juveniles of this rapid and powerful flyer (Milner et al., 1990). The big free-tailed bat is referred to as *Tadarida molossa* and as *Tadarida macrotis* in earlier scientific writings, but it was elevated to the genus *Nyctinomops* based on morphological analysis (Freeman, 1981). Molecular genetic studies have been conducted on this species that confirm its distinctiveness and provide interpretations of its relationships to other species of molossid bats (Ammerman et al., 2012b; Dolman and Ammerman, 2015). There are no named subspecies. Milner et al. (1990) provided a complete taxonomic synonymy of past scientific names for the big free-tailed bat. Another English common name is the Tacubaya free-tailed bat.

HABITATS AND RELATIVE ABUNDANCE.— Big free-tailed bats have been captured in mist nets in a range of habitats in the western United States, including lowland deserts, piñon-juniper, ponderosa pine, and mixed conifer vegetation assemblages ranging to over 2,800 meters in elevation (for example, Borell, 1939; Cockrum and Ordway, 1959; Zimmerman, 1970; Jones and Suttkus, 1972; Easterla, 1973; Carothers and Ruffner, 1974). However the distribution seems localized. A few areas have been documented where they are likely to be taken in surveys, but they are rare in many other surveyed areas within the general distribution. They have not been captured in several intensive mist-netting surveys within their general distribution (for example, Black, 1974; Cockrum et al., 1996; O'Shea et al., 2011a; Geluso and Geluso, 2012; Jones, 2016), again suggesting only localized abundance. In a few other studies, this species has not been captured but has been detected based on vocalizations or echolocation, perhaps at significant distances from roosts.



Base map: Includes geospatial data 'World Countries' and 'World Ocean Background' from ESRI, Redlands, California.

Data source: North American Bat Ranges, compiled by Bat Conservation International, digitally available at www.data.gov.

Coordinate System: North America Lambert Conformal Conic
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 0.0000
False Northing: 0.0000
Central Meridian: -96.0000
Standard Parallel 1: 20.0000
Standard Parallel 2: 60.0000

FIGURE 40. Approximate distribution of the big free-tailed bat, *Nyctinomops macrotis*. Species range is shown in yellow, but also includes much of southern Mexico through most of northern and central South America and the Greater Antilles (see text).

Arizona*:* Big free-tailed bats ranked as least captured (one bat among 353 individuals of 15 species) in ponderosa pine forests at 1,350 to 1,930 meters elevation along the East Verde River below the Mogollon Rim on the Tonto National Forest in central Arizona (Lutch, 1996). In northern Arizona, this species was captured in several regions in mist nets placed over large stock ponds (14 by 18 meters or greater in size; smaller sizes did not yield captures) at elevations ranging from 870 to 2,700 meters in habitats ranging from Great Basin desert vegetation to spruce-fir forests (Corbett et al., 2008). Five bats radio tracked in one area during nightly flights were located over desert scrub vegetation and to a lesser extent piñon-juniper woodlands and ponderosa pine forest, and used canyons and edges of plateaus as travel corridors (Corbett et al., 2008). They ranked thirteenth in abundance among 17 species of bats (five captured of 1,171 total bats netted) taken over water in mostly ponderosa pine and piñon-juniper habitats of the Arizona Strip in northwestern Arizona (Herder, 1998).

California and Nevada: Records of big free-tailed bats in California have been very rare, without captures in mist nets and with few presumed acoustic records (Pierson and Rainey, 1998c). They were only detected acoustically in one sample at the Nevada Test Site, although over 2,000 individuals of 14 other species were documented with mist nets (Hall, 2000).

Colorado and Utah: None were captured in a mist-netting survey over water at Mesa Verde National Park in southwestern Colorado during which 1,996 individuals of 15 species were captured, but hundreds of passes were recorded by ultrasonic detectors throughout the summer (O'Shea et al., 2011a). Echolocation calls of this species also were recorded without capture in multiple canyons elsewhere in southwestern Colorado (Navo and Gore, 2001). In far western Colorado, this species ranked thirteenth in relative abundance of 16 species (4 captures among 899 bats) at Colorado National Monument and the adjacent McInnis Canyons National Conservation Area during three summers of netting; nets were placed over small ephemeral pools in deep slickrock canyons within primarily piñon-juniper woodland and riparian habitats (Neubaum, 2017). Big free-tailed bats were uncommon on the Colorado Plateau of the Four Corners Region, but they can be abundant at localized capture sites in the general vicinity of roosts in cliffs (Mollhagen and Bogan, 2016). At Arch Canyon on the Colorado Plateau in southeastern Utah, they were the second most abundant species captured in mist nets, with 69 bats captured among 295 individuals of 15 species taken at elevations ranging from 1,474 to 1,707 meters; a large colony was known to roost in cliffs in the region (Mollhagen and Bogan, 2016).

New Mexico: Big free-tailed bats were least frequently captured (a total of one) among 1,595 bats of 20 species taken in the Mogollon Mountains of western New Mexico and adjacent Arizona (Jones, 1965). In a separate analysis limited to three sites over water in western New Mexico and including additional years of sampling, they ranked fifteenth of 19 species (four captures among 1,004 individuals) and were taken at two sites, one site in riparian hardwoods among mesquite-juniper woodlands at 1,465 meters and another site in pine-spruce-fir forest at 2,500 meters elevation (Jones and Suttkus, 1972). Fifteen individuals captured in mist nets over water in the Jemez Mountains of New Mexico were taken in ponderosa pine-mixed conifer forests at elevations of 2,423 and 2,479 meters, ranking ninth in relative abundance among 15 species and 1,532 individuals (Bogan et al., 1998). Echolocation activity of these bats was detected over riparian, conifer, piñon-juniper, and previously (20 years) intensely burned ponderosa pine habitat in the Jemez Mountains (Ellison et al., 2005). A survey that took place at 37 sites across several habitat types in much of New Mexico in 2006 yielded 1,752 bats of 21 species, but only one big free-tailed bat was captured (Geluso, 2006, 2017).

Texas: At one site in Big Bend National Park in southwestern Texas, this was the most abundant species taken in mist nets over water (391 among 1,052 bats of 15 species captured, whereas far fewer were taken elsewhere at Big Bend, leading the investigator (Easterla, 1973) to believe that a maternity colony was located in nearby cliffs (all big-free-tailed bats taken there were adult females or volant juveniles). Overall at Big Bend National Park, Easterla (1973) captured 411 individuals among 4,807 bats of 18 species, ranking fifth in relative abundance when the single site with 391 captures of this species is included. They ranked seventh in relative abundance among 17 species (85 of 1,978 bats captured) during a subsequent survey at Big Bend National Park during 1996–1998 that emphasized lowland habitats, with most captures over open water in river floodplain habitat (Higginbotham and Ammerman, 2002). Big free-tailed bats ranked least abundant among 14 species (one out of 542 individuals) captured in mist nets that sampled at 108 locations over water in northern Chihuahuan desert habitats at Big Bend Ranch State Park in the Trans-Pecos region of Texas; a single bat was captured over water in a sheer canyon with steep, rocky cliffs (Yancey, 1997).

Foraging and Dietary Analysis.— The high aspect ratios and wing loading of big free-tailed bats are analogous to those of fast flying aerial insectivorous birds with foraging habits like swifts and swallows (Vaughan, 1966). Like other molossid bats, they often fly at higher altitudes above ground where fewer obstructions exist to interfere with their less-maneuverable flight. Five were successfully radio tracked to determine the extent of nightly movements (including foraging) in rugged terrain at House Rock Valley in northern Arizona (Corbett et al., 2008). Flight speeds of at least 61 kilometers per hour were measured, with bats ranging as far as 36 kilometers from roosts. An activity area was estimated for one of the females tracked for six nights: she covered 29,590 hectares while foraging, a much larger area than reported for other species of bats but perhaps typical for big free-tailed bats in the region (Corbett et al., 2008). In Mexico City, they have been documented to forage widely over urban areas based on echolocation activity, but they favored large parks, forests, and illuminated areas; these favored habitats had greater insect abundance than other areas, and it was noted that the design of the echolocation calls of this species allows detection of prey at longer distances in open areas such as the airspace over these urban features (Avila-Flores and Fenton, 2005).

Morphological specializations of the head and limited information on food habits would suggest that this species feeds primarily on moths (Freeman, 1979, 1981). Macrolepidopteran moths (probably sphinx moths) were the only group detected in the gastrointestinal tract of the single specimen examined by Ross (1964, 1967). In the most extensive study of stomach contents, Easterla and Whitaker (1972) examined 49 individuals from Big Bend National Park in Texas and also found large moths to be by far the most important dietary component (at 86% proportional volume), but they also noted the presence of more terrestrial insects (crickets and katydids, families Gryllidae and Tettigoniidae) at up to 50% volume in 14 stomachs; two individuals contained largely ants (Formicidae). Freeman (1981) found moth parts to be the dominant prey items that could be identified in fecal samples from four individuals. Debelica et al. (2006) examined fecal pellets from 40 individuals captured at Big Bend National Park during the months of May-September in 2001 and 2002. They reported similar diets to those documented by Easterla and Whitaker (1972) from the same region over 30 years earlier, with lepidopterans the dominant item (about 87%) and other orders constituting less than 5% each by volume. Sparks and Valdez (2003) found a more varied diet in analysis of fecal pellets from below a roost in northern New Mexico, where although lepidopterans were the most frequently occurring group, the most important food items by proportional volumes were homopterans (cicadellid leafhoppers) and hymenopterans (ichneumonid wasps), followed by lepidopterans, hemipterans, and dipterans. It is possible that some of the smaller, weaker fliers among insect groups reported in dietary analyses are swept aloft by rising air currents.

Roosting Habits.— Winter Roosts: Winter roosts of big free-tailed bats in the U.S. are unknown. Records of occurrence during winter are rare compared to summer. Although they are capable of torpor (LaVal, 1973), some sources suggest that these bats migrate long distances seasonally, whereas others note that it is not clearly known whether they migrate or hibernate locally (for example, Higginbotham and Ammerman, 2002; Ammerman et al., 2012a). Poché (1979) noted substantial fat deposition in September in southwestern Utah, with multiple captures during late May through mid-September but no captures during other months.

Warm Season Roosts: In the United States, the big free-tailed bat is primarily a dweller of crevices in cliff faces, although use of tree cavities and buildings is known in other countries to the south (Milner et al., 1990). The very few roosting sites discovered thus far in the U.S. have been in rock crevices, particularly in cliffs of steep-walled canyons (e.g., Borell, 1939; Poché, 1979; Bogan et al., 1998; Navo and Gore, 2001). Borell (1939) reported the first colony known from the United States, discovered in a canyon in the Chisos Mountains of southwestern Texas (elevation 1,890 meters) based on loud daytime vocalizations emanating from a high rock crevice (Borell, 1939). About 130 were housed in the small horizontal crevice (about six meters long and 15 centimeters wide) located about 13 meters above the talus slope of a sheer cliff wall (Borell, 1939). A presumed nursery colony also was reported from a vertical rock crevice formed by an exfoliating rock slab about 13 meters above a canyon floor in Chihuahua, Mexico near Big Bend National Park, Texas, where additional colonies in crevices in canyon walls were reported (Easterla, 1972, 1973). Many of the mist-netting records also have been in the vicinity of habitat with cliffs within canyons (Easterla, 1973; LaVal, 1973; Mollhagen and Bogan, 2016), as have the few acoustic survey records in California (Pierson and Rainey, 1998c).

Poché (1979) reported a colony of about 150 of these bats in a crevice in a cliff in southwestern Utah during summer. A maternity colony in a rock crevice along the Los Pinos River in northwestern New Mexico and a maternity colony "under slabs of lava on a perpendicular lava cliff" in central New Mexico discovered by hearing loud daytime vocalizations were reported by Findley et al. (1975:70). In the Jemez Mountains of north-central New Mexico, five lactating females were radio tracked to colonies in five south and east facing roosts in rock crevices, nine to 35 meters above the bases of high canyon walls at elevations ranging 1,921 to 2,311 meters (Bogan et al., 1998). Emergence counts in the Jemez Mountains study averaged 100 bats per roost (range six to over 220 bats); radio-tagged bats ranged far from roosts, which were located 11–30 kilometers from the point of capture (Bogan et al., 1998).

Seven radio-tracked adult females led to the discovery of three roosts in the rugged habitats of far northern Arizona (Corbett et al., 2008). Roosts were in large, vertical crevices in tall (30 to 152 meters) cliffs of south or southeast facing canyon walls at distances ranging from 1.9 to 23.2 kilometers from points of capture over stock ponds (roosts are described in greater detail by Corbett et al., 2008); four bats exited one of these roosts, but estimates of colony size were not possible at other roosts (Corbett et al., 2008). In southwestern Colorado, three adjacent roosts in crevices in canyon walls above the Dolores River were discovered in summer of 1998 after investigators heard loud daytime vocalizations; 25 individuals were seen emerging from the only crevice where conditions permitted observation (Navo and Gore, 2001). Neubaum (2017) located three roosts in crevices in large cliffs in western Colorado, two found opportunistically and one by radio tracking a non-reproductive female. Counts at emergence at the three roosts ranged from at least thirteen to 64 bats. A maternity colony is also known from a canyon in southeastern Colorado (Navo and Gore, 2001). Pierson and Rainey (1998c) noted the likely existence of a roost in a rock crevice high on a cliff face in San Diego County, California.

There are records of two specimens of big free-tailed bats from buildings in San Diego, California, neither suggestive of use as a roost: one had likely become entrapped in a 23 meters tall tower (Huey, 1932), and a second was found hanging in a second story hallway (Huey, 1954b). One big free-tailed bat was taken at a building in western Colorado (Neubaum, 2017).

POPULATION ECOLOGY.— Litter Size, Natality, and Female Reproduction: Eight females from a colony in the Chisos Mountains of Big Bend National Park in western Texas taken in 1937 contained one embryo each (Borell, 1939). Seventeen females from elsewhere in Big Bend National Park each had a single embryo (Easterla, 1973). One female from the Chiricahua Mountains of southeastern Arizona and one female from the Trans-Pecos region of Texas each held single embryos (Cockrum and Ordway, 1959; Yancey, 1997). One female from Chihuahua, Mexico also had a single embryo (Bradley and Mauer, 1965).

Twelve of 15 (80%) adult female big free-tailed bats captured in the Jemez Mountains of New Mexico were reproductive in 1996 and 1997 (Bogan et al., 1998). Natality in a sample of 170 adult females from Big Bend National Park in Texas during 1967–1971 was 85% (26 non-reproductive; Easterla, 1973). In a subsequent study at the park, natality was about 74% (approximately 57 of 77 females were reproductive; Higginbotham and Ammerman, 2002). Eight of 10 adult females examined by Borell (1939) in western Texas were reproductive (80% natality). Constantine (1961b) found 90% natality in 30 adult females examined in northern New Mexico during 1958, and LaVal (1973) reported that eight of 12 (67%) females taken over water in the Guadalupe Mountains National Park in western Texas during June were pregnant, with one of two taken in August lactating.

Survival: We are unaware of any published literature with quantitative data on survival for this species.

Mortality Factors: Mortality factors are not well known. Rabies is known in big free-tailed bats (for example, Constantine, 1961b; Armstrong et al., 1994; Pape et al., 1999; Mondul et al., 2003), and they are usually infected with a rabies virus variant that is species-specific (Shankar et al., 2005). Eighteen moribund or dead individuals were found around pools of water at Ghost Ranch, near Abiquiu, New Mexico, during summer 1958; rabies was only tentatively diagnosed in three of the bats and cause of death of the others remained undetermined, with some pathological conditions of unknown etiology observed on necropsy (Constantine, 1961b). The lung fungus *Pneumocystis* has been detected in this species in Brazil (Sanches et al., 2012), as has *Histoplasma capsulatum*, the agent for histoplasmosis (Galvão-Dias et al., 2011). Ectoparasites have been reported as summarized by Sparks and Choate (2000; see also for example, Ritzi et al., 2001; Poché, 1981) but without evidence for associated mortality. Predation on this species in the U.S. has not been recorded in the literature. During summer 1997 in southeastern Utah, two of us (MAB and TJO) observed five peregrine falcons alight on a cliff-top above a crevice-roosting colony of several hundred big free-tailed bats at sunset, then repeatedly swoop among the emerging bats and at times were successful in capturing them. Accidental death due to ensnarement on a locust spine was documented at Grand Canyon National Park in Arizona (Guse, 1974). They have been found dead beneath wind turbines in northern Arizona (Thompson and Bay, 2012).

Population Trend: Big free-tailed bats aggregate into maternity colonies of moderate numbers for rearing young, but locations of breeding colonies in the United States are poorly known. One colony of an estimated 150 females was discovered in a horizontal crevice in a cliff in Big Bend National Park in 1937 (Borell, 1939); a colony of unknown size was reported to still be present at the site in 1958, thought by Davis and Schmidly (1994) to be the only known nursery colony of this species in the United States. This colony was not located again in subsequent attempts (Schmidly, 1991). A nursery colony was also suspected to exist in Guadalupe Mountains National Park in Texas based on the presence of 14 females (nine reproductive) and no males netted over water in 1968 and 1970 (LaVal, 1973), but subsequent work could not confirm the existence of a resident colony (Genoways et al., 1979). Easterla (1973) reported a few colonies in cliffs in Big Bend National Park in Texas, and at least two colonies were known from New Mexico (Findley et al., 1975). As noted above under the section on roosting habits, more-recent studies have confirmed the presence of a few maternity colonies in Arizona (Corbett et al., 2008), Colorado (Navo and Gore, 2001; Neubaum, 2017), New Mexico (Bogan et al., 1998), and Utah (Mollhagen and Bogan, 2016). None of these colony sites have been regularly monitored since their discovery.

Management Practices and Concerns.— In northern Arizona and similar arid areas subject to drought, maintenance of larger (at least 14 meters diameter) artificial ponds by land managers for grazing livestock is important for provision of water resources for big free-tailed bats (Corbett et al., 2008), perhaps especially for lactating females. Similar recommendations are applicable to other areas within the range of this and other species of concern. Too little is known about the ecology of this species to predict consequences of various other land management practices on their populations. The need for high, steep cliffs for breeding would suggest curtailment of human activities that could cause disturbance (such as blasting or recreational climbing) might be considered near such locations in the known breeding range, especially during summer months when maternity colonies are active. Major impoundments could also flood cliff habitats. These bats are represented in museum collections from the United States only in small numbers, and requests for permits for scientific collecting should be reviewed carefully to insure that the activities do not pose a direct threat to colonies. Such was the case in the past. Davis (1974), for example, reported acquiring specimens in 1958 by shooting a shotgun several times into the rock crevice occupied by female big free-tailed bats in Texas, at the time the only known breeding colony in the United States.

Summary and Highlights

The amount of information that has been developed about the bat species of concern over the past two decades since their informal designation by the U.S. Fish and Wildlife Service (1996a,b) is impressive. We believe that several factors have come into play in fostering this increase in knowledge. One of the primary factors is the highlighting of these species with this designation by state and federal agencies, and by non-governmental conservation organizations. This focus also has benefitted by the general increase in public and scientific interest in bat biology and conservation, and by advances in research technology available for application to studies of these species of concern. Advances include miniaturization of radio transmitters for telemetry, development of field acoustic sampling, applications of molecular genetics, and ever-more sophisticated methods of quantitative analysis and statistical modeling. It is likely that new technological advances will continue to be applied toward better understanding of these species.

Despite advances in knowledge and application of new scientific approaches to research, the degree of new information available is unevenly spread among topics and species. As an index to recent research, we compiled the numbers of recent papers (2007–2016) we reviewed that were based on original data and focused on warm-season roosting habits. Little new information has been published about the two bat species of concern in American Samoa and the Caribbean trust territories: we found only two papers with original data published on the Samoan flying fox over the past decade, and two concerning the red fruit bat. Both of these species roost on tree branches in tropical forests. The remaining 18 species of concern in the 50 states were the subjects of about 320 papers and reports with original data. Even these, however, are unevenly spread among species, depending in part on distribution and roosting habits. For example, very little is known about western species of concern that roost in high cliffs, and much more is known about hibernation in species that regularly aggregate in caves and mines than species that apparently do not. Below we summarize and highlight features that have emerged from each of our major review topics.

Conservation Status.— International status designations by the International Union for the Conservation of Nature and NatureServe are less inclusive of the species of concern than designations by federal and state agencies within the U.S., in part because these organizations may consider the full range of species distributions beyond the U.S. borders, may rely on different category definitions, or in part may rely on opinions of different experts. The International Union for the Conservation of Nature designated the red fruit bat as "Vulnerable" and two species were placed in the lesser category "Near Threatened" (the Samoan flying fox and the Mexican long-tongued bat); the other 17 species were designated as "Least Concern". NatureServe regards three of the 18 species within the contiguous U.S. as "Vulnerable" (Rafinesque's big-eared bats, California leaf-nosed bat, and Mexican long-tongued bat). The other 15 species are regarded as "Secure" or "Apparently Secure", but subspecies of two of these are designated as "Critically Imperiled" (*Myotis yumanensis oxalis, M. thysanodes pahasapensis, M. t. vespertinus*). As noted in the species accounts of these two species, the validity of these subspecies designations has not been investigated with modern genetic approaches.

National status designations by federal agencies are variable for the species of concern. The U.S. Forest Service applies "Sensitive Species" status largely by administrative region, as does the Bureau of Land Management (by state office), and some species may be designated as sensitive in some regions or states but not others. Details are available at those agencies. The U.S. Forest Service regards at least 10 of the species of concern as Sensitive Species (including the red fruit bat in Puerto Rico). The Bureau of Land Management designates 14 species of concern as Sensitive, all in western states, but species designations vary among state offices.

Many states have designated the bats described in this volume as having special status. One of the facilitating mechanisms for these designations stems from the federal Wildlife Conservation and Restoration and State Wildlife Grants programs defined by the U.S. Congress under legislation enacted in the year 2000 (114 Stat. 2762A–118 Public Law 106–553—Appendix B; see U.S. Government Printing Office, 2000). The law made funding available to the states and territories for wildlife conservation, provided that each state develop a State Wildlife Action Plan. Elements required under each plan result in identification of "species of greatest conservation need". Most of the state designations that we compiled fall under that category as a result of this requirement for access to federal funding, but may also include special designations under separate state laws. Forty-five of the 50 states, plus the District of Columbia, Puerto Rico, and American Samoa, give special status to one or more (up to 13) species discussed in this volume. The remaining five states (Hawaii, Iowa, Michigan, Minnesota, and Wisconsin) and some of the other territories include species of bats that are considered endangered or threatened under federal law. Concern about the status of bats is widespread throughout the U.S.

The number of states with special status designations for each species of concern varies by the distribution of each species and by overall bat diversity. Species with widespread distributions have such designations in greater numbers of states (for example, the eastern small-footed myotis is designated with special status by 25 states and the District of Columbia, Rafinesque's big-eared bat by 19 states, the southeastern myotis by 17 states, and Townsend's big-eared bat by 16 states). Species with more-limited distributions are designated with special status by fewer states (for example, Underwood's bonneted bat is only recognized with special status by Arizona, and the California leaf-nosed bat, Mexican long-tongued bat, and Arizona myotis have special status in three states). Some species are not designated as special status throughout their distributions across state boundaries (for example, the northern edge of the distribution of the Arizona myotis occurs in southern Colorado, but it is not assigned special status in that state); some species are given special status by states at the edges of their distribution (where they may tend to be rare) but not by some states at the core of the range (for example, the long-legged myotis). States with greater diversity of bats tend to have greater numbers of species of bats with special status designations (for example, Arizona, California, and Texas), and those states with lower diversity of bats may have just a single special status species (for example, Maine, Delaware, Massachusetts).

Description, Distribution and Systematics.— Most of the species of concern are relatively distinctive in appearance, but a few are more difficult to discriminate and require some expertise. Less-experienced readers should consult local experts in mammalogy for assistance, and in cases where identification may be in doubt, collection of a few voucher specimens is advisable. Difficulties in identification mostly apply to species of *Myotis*. In some areas, even experts must take care in differentiating Yuma myotis (*M. yumanensis*) from little brown myotis (*M. lucifugus*), or western small-footed myotis (*M. ciliolabrum*) from California myotis (*M. californicus*; see species accounts for details). Distributions of species are fairly well-defined in broadest outlines, but within those outlines local and regional occurrences can be poorly known, and new locality records continue to be accrued for species of concern. New basic surveys of bat faunas of areas under various management jurisdictions can yield such information. New state records (for example, Adams and Lambeth, 2015) and more anomalous locality records of likely wandering individuals (for example, Caire and Loucks, 2013) continue to be documented. Distributions of species are not static. For example, interesting changes in distribution of the species of concern are likely to occur over time with climate change.

Refinements in knowledge of species taxonomy also are likely to occur. Although the nomenclature of most species of concern appears fairly stable, future changes can be expected given new insights that may be provided through advances in molecular techniques and quantitative systematic analyses. Multiple examples of changes in understanding of taxonomy within the bat fauna of the U.S. within the past 35 years suggest that more will occur in the future. As examples, names of the following U.S. species of concern all had been changed since 1981: *Corynorhinus rafinesquii, Corynorhinus townsendii, Idionycteris phyllotis*, *Myotis ciliolabrum*, and *Nyctinomops macrotis*. The validity of sub-specific designations and nomenclature will likely be subject to change as well (for example, Piaggio and Perkins, 2005; Piaggio et al., 2011).

Habitats and Relative Abundance.— The species of concern vary in both general and more specific types of habitats used. Based on literature reviews in the species accounts, we found it useful to group each species within general habitat types, with qualitative judgements about more specific habitats nested by species within these general habitats (Table 3). These categories are qualitative and are largely based on results of disparate mist netting surveys, usually conducted without prior design for comparisons among studies. We acknowledge that many factors can influence the relative abundance and species composition of bat communities and that these factors are poorly known in most surveys (see Introduction and Objectives sections). One of these may be susceptibility to capture in mist nets based on constraints imposed by wing morphology on maneuverability and agility. Based on those factors alone, however, results of many surveys are inconsistent with predictions. In the western U.S., for example, less-maneuverable species (high wing loading and high aspect ratio) such as big free-tailed bats and greater bonneted bats (Norberg and Rayner, 1987) are seldom captured in mist nets except where colonies are known or subsequently found to be located in nearby cliffs. In other surveys, species that are known to be highly maneuverable and which roost in smaller colonies dispersed across the landscape, such as many of the vespertilionids, can rank high in abundance. These rankings can be highly variable among surveys, best illustrated by the western coniferous forest and woodland species of *Myotis* (see below).

The two species of concern on island territories generally use tropical rain forest. Habitat use by the red fruit bat (*S. rufum*) in the U.S. Virgin Islands is not as well-understood as in Puerto Rico, where they are mostly known from a narrow range of elevations of a specific forest type. Species within the U.S. are found in different general habitats, where more specific habitats often seem to be associated with roost availability. Three species primarily use forests in the eastern U.S., with two considered abundant in southern bottomland hardwood forests where they roost in hollow trees (Rafinesque's big-eared bat and the southeastern myotis). One species (the eastern small-footed myotis) primarily uses upland forests, often in mountainous terrain with talus-like rock features and caves available as roosts. Three species are characteristic of southwestern arid lowlands in the U.S.: the California leaf-nosed bat often uses desert washes in scrub habitats in the vicinity of old mines or caves; Underwood's bonneted bat is limited to a very small area of Sonoran desert in Arizona near the Mexican border, where they seem to prefer roosting in cavities in saguaro cactus; and the nectar and fruit feeding Mexican long-tongued bat, a seasonal migrant that occupies a number of vegetation types (often in woodlands near riparian areas) that overlap the distribution of agaves and columnar cacti. A third category of habitats includes three species of bats that use a wide variety of habitats and elevations in the western U.S. that are within commuting distances of high cliffs and canyons that provide their principal known roosts (spotted bat, greater bonneted bat, and the big free-tailed bat).

Western coniferous forest and woodland provides a fourth broad category of general habitat used by four species of myotis (western small-footed myotis, long-eared myotis, long-legged myotis, and fringed myotis). Use of specific habitats within these forests appears to be regionally or locally quite variable with specific affinities sometimes difficult to judge. The species composition of bats in these western forests can include all four species, but relative abundance can vary radically. For example, long-eared myotis ranked as most abundant in two surveys in ponderosa pine forest and scrubland habitats in northeastern Oregon and south Central Washington (among 11 species and 1,470 individuals captured), but they were much lower in relative abundance in moist forests farther west in those states. They ranked relatively low in abundance in surveys in California and Nevada but were the most abundant species over the course of a 34-year study at a site in the San Mateo Mountains of New Mexico that entailed the capture of 1,390 individuals of 11 species, but with fluctuations in year-to-year abundance; they were second-most abundant in a shorter-term study elsewhere in the same mountain range, yet were low to intermediate in abundance in other studies including forests and woodlands in New Mexico. Long-eared myotis were the most abundant or second-most abundant species in studies in ponderosa pine and piñon-juniper woodland in southwestern Colorado, but they were seldom captured at higher-elevation habitats in lodgepole pine and Douglas fir/mixed conifer forests of Colorado and were of lesser abundance on the eastern side of the Rocky Mountains in primarily ponderosa pine and Douglas fir/mixed conifer forests. The long-legged myotis, in contrast, was captured in a wide variety of western habitats and was usually the most abundant species in higher-elevation forests. However, long-legged myotis also ranked high in relative abundance in several studies across a variety of lower, drier habitats in a wide range of states ranging from Arizona and New Mexico north and east through the central rocky mountain states and western Great Plains, but not in California or in moist forests in the western coastal mountains of Oregon and Washington. Western small-footed myotis and fringed myotis (the latter species characterized in the same agility group as long-eared myotis by Norberg and Rayner, 1987), with few exceptions, generally ranked low to intermediate in relative abundance in surveys throughout their distribution.

We placed two western species of concern in a separate category as primarily found with greatest abundance in riparian habitats (Arizona myotis and Yuma myotis), but these species also vary

TABLE 3. Summary of habitat types of known importance to species of concern. See species accounts for greater detail and literature citations.

Typical General Habitat	Species	Habitats of Seemingly Greatest Importance for the Species
Tropical Forest	Samoan flying fox	Mature primary rain forest in Samoa Islands
Tropical Forest	Red fruit bat	Lower elevation tabonuco (*Dacryodes excelsa*) rain forest (El Yunque National Forest, Puerto Rico), remnant mixed evergreen-deciduous forest on Vieques Island (Puerto Rico). Local and patchy, nowhere abundant.
Eastern U.S. Forests	Rafinesque's big-eared bat	Bottomland hardwood forests with suitable roosts
	Southeastern myotis	Bottomland hardwood forests with suitable roosts throughout the distribution, karst areas at the southern and northern limits
	Eastern small-footed myotis	Upland forests, especially in mountainous terrain near ground-level roosts in talus-like areas or caves
Southwestern Arid Lowlands	Mexican long-tongued bat	Various vegetation zones (especially woodlands) within the distribution of agaves and columnar cacti, often near riparian zones. Seasonal.
	Underwood's bonneted bat	Sonoran Desert and mesquite-grassland in extreme southern Arizona. Other habitats used in countries south of the U.S.
	California leaf-nosed bat	Desert scrub, especially desert washes near suitable roosting habitat in old mines and caves
Western Uplands with Cliffs and Canyons	Spotted bat	Multiple broad habitat types from desert to montane, but patchily distributed, probably in relation to availability of roosting habitat in crevices in high cliffs
	Greater bonneted bat	Multiple broad habitat types from desert to montane, but patchily distributed, probably in relation to availability of roosting habitat in crevices in high cliffs
	Big free-tailed bat	Multiple broad habitat types from desert to montane, but patchily distributed, probably in relation to availability of roosting habitat in crevices in high cliffs
Western Coniferous Forests and Woodlands	Western small-footed myotis	Primarily mid-elevation woodlands and forests
	Long-eared myotis	Primarily mid-elevation woodlands and forests, especially relatively dry ponderosa pine and piñon-juniper woodland
	Fringed myotis	Ponderosa pine forest, usually much lower relative abundance in other habitats
	Long-legged myotis	Multiple broad habitats from near sea level to montane, often most abundant in inland forests at higher elevations in ponderosa pine forests and above.
Western Riparian Habitats	Yuma myotis	Multiple broad habitats, highest in relative abundance near plentiful permanent water. Ranks high in relative abundance in surveys in parts of California, lower elsewhere.
	Arizona myotis	Multiple broad habitat types from desert to montane, usually near abundant permanent water.
Other	Townsend's big-eared bat	Multiple broad habitat types from desert to montane, but patchily distributed, probably in relation to availability of old mines and caves as roosting habitat.
	Cave myotis	Grasslands dissected by small canyons and riparian woodlands in lower western Great Plains and in deserts at lower, warmer elevations in the southwestern U.S., within flight distance to permanent water. Nowhere high in abundance except near roosts.
	Allen's big-eared bat	Multiple broad habitat types from desert to montane, especially middle-elevation forests and woodlands. Patchily distributed but not in clear association with specific roost types and never in abundance. Perhaps local abundance may vary in relation to availability of roosting habitat in crevices in high cliffs, but also roosts under tree bark of snags and in caves and tunnels.

widely in relative abundance among surveys and regions. A final category of “other” was used for three species of western bats that do not rank high in relative abundance in surveys, and that have local distributions dependent on the distributions of caves or old mines over a variety of habitats in two cases (Townsend’s big-eared bat and cave myotis) and on undefined factors in the case of the third and little-studied species (Allen’s big-eared bat).

FORAGING AND DIETARY ANALYSIS.— The different species of concern encompass a wide variety of food habits, ranging from frugivory and nectar-feeding (Samoan flying fox, red fruit bat, and Mexican long-tongued bat) to various styles of insect feeding in the remaining species. For the insectivorous species, dietary analyses have resulted in descriptions of insect prey classified by order or family for each, with some species more thoroughly investigated than others. Tendencies to focus on certain groups and sizes of prey vary with species, but dietary studies and feeding observations also have shown that some of the insectivorous species of concern are opportunistic in taking prey, and that prey types can vary among regions.

Earlier studies focused on accurate qualitative descriptions of bat foraging made through careful naturalistic observations. These descriptions revealed a diversity of foraging styles among insectivorous species, ranging from those that feed close to and sometimes glean prey from the ground (California leaf-nosed bat) to those thought to forage at great heights on insects swept aloft by rising air currents (greater bonneted bat) or that forage mainly over the surfaces of permanent water (Yuma myotis). Species also differ in their proclivities to ‘hawk’ insects in the open air or to forage very close to vegetation. Naturalistic observations have been augmented over the past 20 years by radio-tracking studies and use of acoustic sampling. In particular, tracking studies have resulted in more detailed observations pertinent to the sizes of foraging areas and distances traveled from roosts by foraging bats over the short lives of radio transmitters (one to two weeks), traits that also vary greatly among the few species studied. Distances from roosts traveled by foraging bats range from maxima of 43–50 kilometers for spotted bats to 1.8 kilometers for the eastern small-footed myotis. Foraging home range areas include estimates of 2.1 hectares for the red fruit bat, 38 hectares for the long-eared myotis, 10–100 hectares for the eastern small-footed myotis, two to 225 hectares for Rafinesque’s big-eared bat, 304–647 hectares for the long-legged myotis, two to eight square kilometers for the Samoan flying fox, an average of 297 square kilometers in spotted bats, and up to 474 square kilometers for Underwood’s bonneted bat.

ROOSTING HABITS.— Based on our reviews of roosting habits that appear in the species accounts, considerable amounts of information have been learned on multiple levels about roost use by “forest bats” that roost primarily in hollow trees in bottomland hardwoods (Rafinesque’s big-eared bat and southeastern myotis; about 60 papers) and to some extent in snags and under bark in various western forests (Allen’s big-eared bat, Arizona myotis, long-legged myotis, fringed myotis, long-eared myotis, Yuma myotis; about 140 papers). The increase in information about roosts of these species is tied directly to the interest in improving forest management practices to benefit bats. Perhaps somewhat unanticipated, in some areas western forest bats were often tracked to roosts in rock crevices rather than roosts in trees and snags (see corresponding species accounts for details).

Less information has accrued about species that do not roost in trees and snags. Far fewer papers have appeared during the most recent decade on species known primarily to roost in rock crevices on cliff faces (spotted bats, greater bonneted bats, and big free-tailed bats; 18 papers). Increasing information has been accruing on the two species that roost in small crevices in rocks, soil, and under talus (eastern and western small-footed myotis; 46 papers). Three species that roost primarily in caves and abandoned mines varied greatly in numbers of recent papers: Townsend’s big-eared bats were the subject of 36 papers, cave myotis of 16 papers, and we found only a single available report on roosting of California leaf-nosed bats published during 2007–2016. Two species limited in distribution to Arizona or Arizona and New Mexico (Underwood's bonneted bat and Mexican long-tongued bat) were the subjects of only one paper about roosting over the last 10 years.

Radio telemetry has played a key role in gaining knowledge about roosting habits of species of concern. The number of individual bats radio tracked among the various species of concern mirrors this general increase in knowledge, with most applications involving three species of forest bats. Based on papers reviewed in the species accounts, we estimate that the following number of individuals have been radio tagged to determine roost locations (and to a lesser extent foraging habits): more than 310 long-legged myotis, more than 290 Rafinesque's big-eared bats, and more than 200 long-eared myotis. Minimum number of bats radio tagged range from 30 to 100 for five species: fringed myotis, Arizona myotis, Townsend's big-eared bat, spotted bat, and red fruit bat (in descending order). From 10 to 30 individuals were tagged in studies of western small-footed myotis, eastern small-footed myotis, Yuma myotis, Allen's big-eared bat, and the big-free tailed bat. From three to seven individuals were tagged in tracking studies of southeastern myotis, Samoan flying fox, Underwood's bonneted bat, and the greater bonneted bat. We found no recent published or publicly accessible papers available on radio tracking of the California leaf-nosed bat, the cave myotis, or the Mexican long-tongued bat.

Most of the telemetry-based roosting studies concentrated on adult females during summer, with the objective of understanding roost use for birthing and rearing young. During the summer maternity season, females of the U.S. species of bats that spend the warmer seasons in trees usually roost in basal hollows, cracks, cavities, or under bark in relatively small groups, and they change roosting trees on average every one to three days (well demonstrated for Rafinesque's big-eared bats, long-eared myotis, fringed myotis, and long-legged myotis). The three species of *Myotis* that are in this group also frequently roost in rock crevices, where they also switch roosts at a similar frequency, as do Arizona myotis using trees as roosts. Colonies tend to use many different roosts within a core area that will vary by species. The high frequencies of roost switching are characteristic of the fission-fusion social systems of many bats, and result in group sizes that vary greatly. In the case of the above species roosting in trees or rock crevices, maternity group sizes are typically small but will vary from day to day and among study areas. Some typical group sizes and maxima when roosting in trees are: Rafinesque's big-eared bats (six to 40; 100), Allen's big-eared bat (two to 13; 21), long-eared myotis (one to four; 14), fringed myotis (one to 35; 118), long-legged myotis (two to 50; 459), and Arizona myotis (one to 180; 500). Where studied, males of these species tend to roost solitarily but also change roosts frequently.

Roost switching is less well-known for species of concern that do not commonly roost in trees. High frequencies (every one to two days) of roost switching also characterize the eastern and western small-footed myotis that roost under rocks, in talus, or in soil crevices during summer. Group sizes in both of the latter species are small (ranging one to 20, typically less than five) during summer. Few of the species that roost in crevices in high cliffs (spotted bat, greater bonnet bat, big free-tailed bat) have been studied intensively, but they seem to shift roosts less frequently than the above species and occur in small groups of one to 30 spotted bats, up to 100 greater bonneted bats, and up to 220 big free-tailed bats. Cave-dwelling species are not well studied because of attenuation of radio signals within interior chambers underground, but they also do not seem to switch roosts frequently; they can be found in maternity groups ranging from a few dozen or fewer (Mexican long-tongued bats), a few hundred at most (Townsend's big-eared bats), a few thousand (California leaf-nosed bats) to tens of thousands or more (cave myotis and southeastern myotis). Non-telemetry based surveys indicated shifting of roost locations in Townsend's big-eared bats in areas with multiple and complex abandoned mines. Individuals roosting in cavities in saguaro cactus seem to live in very small groups (up to five) and also switch roosts nearly daily, but are in need of much more study.

The bats that roost primarily in caves during summer also overwinter in caves, depending on region (Rafinesque's big-eared bats and southeastern myotis do not hibernate in caves in southern areas but do so in northern areas of their distributions). Cave myotis (hibernators), Townsend's big-eared bats (hibernators), and California leaf-nosed bats (non-hibernators) make local or regional migrations between summer and winter caves in some areas. The Mexican long-tongued bat migrates seasonally and does not hibernate.

Nearly all the species of concern are known to roost in buildings and other human-made structures to some degree. A lack of reports of buildings used as roosts is only the case for the Samoan flying fox, the red fruit bat, Underwood's bonneted bat, and the California leaf-nosed bat (which will use buildings and bridges as night roosts). Buildings are known to be used for maternity groups by 14 of the species of concern.

Winter habits are poorly known for many of the species of concern that roost in rock crevices, under talus, and in cracks in boulders and snags during summer. We suspect that in many cases these bats winter in inconspicuous deep cracks and crevices in rock or compacted soil. Overwintering of big brown bats in such roosts has recently been demonstrated (Neubaum et al., 2006; Lausen and Barclay, 2006; Klüg-Baerwald et al., 2017), and our review fails to indicate significant use of caves as winter hibernacula for most western species of concern that hibernate. Twente (1960:70) offered a speculative explanation that these western species "may hibernate underground or in deep crevices in cliffs which remain cold but above freezing" but had no evidence to support this notion. The likelihood that these species hibernate in situations other than caves also was presaged by Griffin (1945:22) for eastern bats: "There remains a speculative possibility that these bats may use other places than caves for hibernation, at least in areas where caves are lacking. ...Bats would probably be protected from freezing by small deep crevices in rocks such as those used by snakes, or even by woodchuck burrows... The habits of bats are too little known to dismiss the possibility that in caveless areas they may habitually hibernate in unsuspected retreats. Perhaps this possibility may add zest to the future field work that is necessary before the life histories of cave bats can be satisfactorily understood."

Population Ecology.— Although critical for understanding demographic aspects of conservation, data related to population ecology of the species of concern vary by topic and by species, and in some instances are not well known or not based on large samples.

Litter Size, Natality, and Female Reproduction: Most species of bats worldwide have litter sizes of one or two and this extends to the species of concern. Each of the 20 species typically have one young at birth, with the exception of the southeastern myotis (*M. austroriparius*), in which twinning is very common: a mean litter size of 1.9 occurs in southeastern myotis (based on a very large sample), with triplets also reported. Nonetheless, isolated cases of twins and triplets have been reported in six other species (Townsend's big-eared bat, greater bonneted bat, California leaf-nosed bat, western small-footed myotis, cave myotis, and Yuma myotis), perhaps indicating the potential for some minor degree of flexibility in this parameter. Large sample sizes for estimates of litter size are not available for some species and are based on six or fewer females as reported in the primary literature we reviewed for U.S. populations of the spotted bat, Underwood's bonneted bat, Allen's big-eared bat, and the Arizona myotis. Litter size estimates for an additional six U.S. species are based on samples of 15–28 females (Mexican long-tongued bat, Rafinesque's big-eared bat, western small-footed myotis, long-eared myotis, fringed myotis, and big free-tailed bat).

Although litter sizes show low variability among species of concern, two other critical aspects of recruitment through reproduction can be more variable, are not well studied, and can be positively biased by studying reproduction in female bats only at maternity colonies. First among these is natality expressed as the proportion of females that reproduce each year, and second is age at first reproduction. In many species of bats, non-reproductive females do not require the same roosting conditions that are necessary for females raising young, and as seen in some of the species of concern, non-reproductive females can function similar to males in using different foraging and roosting habitats than reproductive females. Thus not all females may be available for sampling at roosts or nearby habitats throughout their adulthood, and the usual assumption that intervals between births are one year may not always be valid. The biases in interpreting reproduction data from samples taken at maternity colonies was recognized nearly 50 years ago by Davis and Barbour (1970:261), who stated "The percentage of reproductive failure, which needs to be known to understand population dynamics, cannot be obtained from nursery colonies." Similarly, although they had limited data to contrast between reproductive rates of females captured at maternity roosts and those captured away from roosts, Barclay et al. (2004:691) noted that "caution should be taken when assessing reproductive rates from colonies and extrapolating to the entire population". Data acquired from long-term studies of tagged individuals have been successfully combined with multistate, robust-design models to provide more reliable estimates of breeding probabilities in other taxa, such as sea turtles (Kendall and Bjorkland, 2001) and manatees (Kendall et al., 2003). Employing these techniques offers a potential way to approach the problem, although we are aware of only two cases where these approaches have been applied to estimating breeding probabilities of U.S. bats, both common species that were studied where they roosted in colonies in buildings (Frick et al., 2010b; O'Shea et al., 2010).

Estimates of the proportion of adult females that reproduce indicate that this is the most variable aspect of recruitment in the species of concern. In our literature review, we noted that studies of several of these species have shown variability in these proportions due to direct and indirect climatic effects, including intense storms (the red fruit bat), drought (western small-footed myotis, long-eared myotis, long-legged myotis), and long periods of cool rainy weather in summer (Yuma myotis). Calculations of the proportion reproductive individuals based on samples taken in mist nets at places (primarily over water) other than at maternity colonies strongly indicate that not all females breed in any given year. Cumulative totals of such data indicated crude proportions of females reproductive for the following seven U.S. species of concern: 77% (68 of 89) for spotted bats, 95% (96 of 101) for Allen's big-eared bats, 56% (96 of 172) for western small-footed myotis (also 56% of 351 females in Alberta, Canada), 68% (412 of 603) for long-eared myotis, 65% (100 of 155) for Arizona myotis, 75% (282 of 375) for fringed myotis, and 42% (383 of 910 bats) for long-legged myotis. Data based on captures over water may also have biases because heavier, pregnant bats may be less able to avoid nets, lactating bats require more water than non-reproductive bats, and in mountainous regions the elevation of a site may influence the proportion of reproductive females.

Female bats are often assumed to give birth at age one year. However, there are no data for this parameter for 13 of the 20 species; simple generalizations of birth at one year without supporting age data appear in the literature for two others (California leaf-nosed bat and Yuma myotis, but with one study noting only 42% of the latter breed as one-year-olds, based on unpublished data of Frick et al. [2007] from California). A generalization that not all first-year females breed appears for one species (long-legged myotis; Druecker, 1972) without supporting age data. Evidence from one-year old bats marked as juveniles is available only for four species of concern: a small proportion of one-year old females give birth in the Arizona myotis (one of 35) and Townsend's big-eared bat (nine of 34), whereas all of 46 marked one-year-old southeastern myotis and all of 39 female cave myotis were reproductive.

Survival: Adult survival is a key demographic parameter in bat population dynamics. Some form of survival estimation has been applied in studies of six species of concern: Townsend's big-eared bat, southeastern myotis, eastern small-footed myotis, Arizona myotis, cave myotis, and Yuma myotis. Four studies conducted during the late 1940s to the early 1960s on Townsend's big-eared bats in California, southeastern myotis in Florida, and cave myotis in the western Great Plains calculated simple return rates (which do not account for capture probability) and are of historical interest in understanding likely survival requirements to maintain stable populations of bats. A study of eastern small-footed myotis banded at a hibernaculum in Ontario from 1941–1962 was the first to use survival estimation techniques that adjusted for capture probability (Cormack-Jolly-Seber approaches) on a species of concern. Findings from that analysis showed differential survival of males, but estimates for females seem unsustainable and likely were biased by factors such as permanent emigration and banding-caused mortality. Use of standard Cormack-Jolly-Seber models that do not explicitly account for emigration may not be appropriate for monitoring situations in which sampling is limited in spatial scope, and such approaches have not been used with species of concern. Two studies calculated survival rates retrospectively without estimating emigration. One was based on historic records of Townsend's big-eared bats banded in 1965–1974 and recaptured through 1980 in Washington hibernacula, and the second on cave myotis banded at multiple caves in Oklahoma during the 1960s and 1970s. Townsend's big-eared bats in the Washington study showed likely differences in survival and capture probabilities by sex as well as time trends, with estimates likely influenced by permanent emigration due to disturbance and banding-related injury or mortality. The study of cave myotis indicated variable capture probabilities with time, higher survival in females, lower survival during the first six months of life, as well as increasing survival over the first half of the lifespan, and then declining survival thereafter. Survival estimates seemed low in cave myotis, perhaps due to documented major catastrophic flooding of caves and freezing events, as well as possible permanent emigration or banding-related mortality.

Two studies used modern estimation and analytical techniques on more recently marked populations of species of concern but without estimation of emigration bias. Survival of banded Arizona myotis roosting in bat boxes in ponderosa pine forests in Arizona was estimated over a seven-year period ending 2012. Survival and capture probabilities in Arizona myotis varied by sex and year, with female estimates higher than in males. Survival in Yuma myotis populations were estimated in colonies roosting in four bridges in California, two in an area subject to a contaminant spill. Apparent survival of adults was unaffected in the spill area and increased at all four roosts over the study period (1992–1996), coinciding with increasing habitat recovery from a prolonged regional drought; juvenile survival in the area not subject to the spill also increased but was always lower than adult survival and was lower in the area of the spill. Survival estimates indicated a growing population when incorporated in a stage-based population model. In general, studies are lacking that explicitly account for the emigration process when estimating bat survival. Well-established, capture-mark-recapture models that model temporary emigration separately from the survival process can provide more unbiased estimates of survival (for example, Kendall et al., 1997), and more complex sampling designs and models have been used to estimate permanent emigration (for example, Lindberg et al., 2001; Kendall et al., 2013). To our knowledge, no survival estimation studies have used such models and designs with a focus on contemporary populations of the bat species of concern.

Mortality Factors: Direct mortality factors impact species of concern, but documentation is largely anecdotal. Weather events probably have the greatest but highly intermittent effects. Flooding of caves used by southeastern myotis has resulted in deaths of tens of thousands of these bats in Florida, as well as of cave myotis in the Great Plains. Deaths of the latter species due to freezing temperatures and rock collapse also have been reported. Cyclones have directly impacted Samoan flying foxes, particularly juveniles, but carcasses were not documented. Post-cyclone hunting and predation on Samoan flying foxes by domestic pigs also occurred but to an unmeasured extent, and this is the only species of concern in which hunting by humans for food has occurred, regardless of storm effects. Red fruit bat populations on Puerto Rico declined after a major hurricane, but deaths were not witnessed. Minor direct mortality of red fruit bats due to wind turbines has been reported, as has minor mortality of eastern small-footed myotis and big free-tailed bats, and single deaths of cave myotis and long-legged myotis.

Disease impacts on mortality of species of concern have not been well quantified. Deaths due to rabies have been documented in almost all species of concern in the states, but generally not on the scale of mass mortality. Deaths due to white-nose syndrome have been reported in eastern small-footed myotis and some counts of this species have declined, but the degree of impact has been more difficult to ascertain than in more common species. DNA of the fungus that causes white-nose syndrome has been reported on Rafinesque's big-eared bats and southeastern myotis (with clinical disease only in the latter), but without quantifiable mortality. Other diseases and parasites have been documented among the various species of concern, but not in association with mortality. Numerous anecdotal accounts exist describing cases of predation by a wide range of birds, mammals, and reptiles on species of concern but without demonstration of consistent major impacts. Results of examinations for the presence of environmental contaminants have only been conducted on a small number of species of concern for some metals (California leaf-nosed bats, cave myotis, eastern small-footed myotis, southeastern myotis, and Yuma myotis) and organochlorine pesticides (California leaf-nosed bats, cave myotis, long-eared myotis, eastern small-footed myotis, and long-legged myotis). Evidence for exposure to organophosphate insecticides was reported for cave myotis. Lethal poisoning by environmental contaminants has not been conclusively demonstrated in any species of concern other than deaths of long-eared myotis and western small-footed myotis due to entrapment in oil sludge pits.

The most consistently reported source of mortality has been deaths from human vandalism and intentional killing, primarily on accessible populations of bats roosting in caves, abandoned mines, or buildings. Mortality of non-volant young bats that fall beneath roosts is also known in some species (especially in roosts over water), although adults will often retrieve fallen young. In the cases where attempts were made to quantify this, neonatal mortality estimates were generally low (one to five percent of young in Arizona and fringed myotis, but up to 12% in southeastern myotis). A mysterious mass mortality event of thousands of cave myotis was reported during the 1950s, but multiple mortality events of unknown etiology are otherwise rarely observed among the species of concern.

Population Trend: Most of the information available on population trend in the species of concern is anecdotal, and likely influenced by the potential bias in the studying and reporting of findings concerning declines and losses. Furthermore, methods for assessing status through counts have historically been subject to logistical and analytical shortcomings. Nonetheless, much of this anecdotal evidence can be compelling. Indices and qualitative assessments have indicated declines due to storm events for Samoan flying foxes and red fruit bats. Information on recurrence of Mexican long-tongued bats at historic roosting sites in Arizona and New Mexico, and spotted bats and Allen's big-eared bats at netting sites in New Mexico, did not indicate population change. Historic locations known for greater bonneted bats in California were revisited during the 1990s and monitored for the distinctive echolocation calls of this species. This survey confirmed their continued occurrence in several regions, absence at some, and added new records. However, few colonies were observed directly, and all colonies were small.

Assessments of potential or historic roosting sites in caves or old mines have resulted in general conclusions of major losses and often revealed an absence of any strong data usable for multiyear trend assessments. These conclusions apply to colonies of Townsend's and Rafinesque's big-eared bats, California leaf-nosed bats, and southeastern myotis. One recent study showing an increasing trend in counts of hibernating Townsend's big-eared bats at hibernacula at Lava Beds National Monument in northern California, however, provides an example of the value of using count data from monitoring efforts in a strong sampling and analytical framework. Limited sampling indicates possible declines in eastern small-footed myotis concurrent with the advent of white-nose syndrome.

One study investigated changes in abundance within an eleven-species bat community based on mist-netting records over a 34-year period at the same pond in the San Mateo Mountains of New Mexico. After statistically adjusting captures for variation in precipitation and year, an apparent increase in abundance was found for long-eared myotis and stability was indicated for long-legged myotis. Other, more short-term (four to seven years) studies have demonstrated the use of capture-recapture techniques for estimating population parameters for Arizona myotis and Yuma myotis. The Yuma myotis study also resulted in estimation of generally positive population growth rates using life-history based models.

In recent years, emphasis on using presence-absence data and occupancy analysis techniques have been applied to development of monitoring studies of bats. These techniques have been used with some promise in studies of roosts of Rafinesque's big-eared bats and southeastern myotis in bottomland hardwood forests of the southern U.S., and mist-netting and echolocation-detection studies in Washington and Oregon. In one study in the Pacific Northwest, these methods were shown to be feasible for long-eared myotis, fringed myotis, long-legged myotis, and Yuma myotis. In a second study, monitoring efforts were conducted during an eight-year period for the western small-footed myotis, long-eared myotis, fringed myotis, long-legged myotis, Yuma myotis, spotted bat, and Townsend's big-eared bat. Only the fringed myotis showed a decline in occurrence probabilities over the eight-year monitoring period.

Future efforts directed toward monitoring population dynamics and demographic changes in bat species of concern may benefit from clearly delineating the spatial extent of local populations or subpopulations. For example, the study detailing survival in a metapopulation of cave myotis in Oklahoma (Humphrey and Oli, 2015) showed how differences in apparent survival between sexes, age groups, and life stages could be discerned at spatial and temporal scales larger than single roost sites and years. As detailed in many of the species accounts, bats often switch between roosts. Most population monitoring efforts have focused on roosts. Spatially defining the boundaries of populations being monitored, as well as directing monitoring efforts toward meta-roosts or multi-colony social groups when possible, will help expand inference that can be made about population growth and survival beyond the limited conclusions that can be drawn from studies focusing on one or a few colony sites.

Population Genetics: Population genetic surveys have been carried out using a variety of methods on populations of the following species of concern: Samoan flying fox, Rafinesque's big-eared bats, Townsend's big-eared bats, spotted bats, California leaf-nosed bats, western small-footed myotis, and cave myotis. These assessments did not indicate dangerously low genetic diversity, although a 1976 study of allozyme variation in California leaf-nosed bats at a single mine indicated low heterozygosity, and diversity may be low in localized populations of Townsend's big-eared bats. Additional population genetic studies of some of these species, as well as the 13 species not yet sampled, could benefit by assessment at more locations and with additional molecular analyses.

MANAGEMENT PRACTICES AND CONCERNS.— Knowledge about the species of concern has resulted in a variety of management concerns and recommendations. Conservation education has been a universal management recommendation. Most other recommendations generally follow the level of study each species has received, and for most species focus mainly on protection of known roosts and management of roosting habitat for the future. However, concern for the two species in American Samoa and the Caribbean focuses on hunting of Samoan flying foxes for food and on effects of cyclones and hurricanes on habitat and population ecology of both species. Effects of the recent (2017) hurricanes on the red fruit bat in the Caribbean have not been reported but are likely to be very severe based on past events. General loss of habitat and disturbance due to human activities also are issues facing these tropical species. Management and education policies favoring well-enforced elimination or regulation of hunting on American Samoa has been a highlighted need, as well as long-term habitat preservation and expansion for both species. Deaths of red fruit bats at wind power facilities was recently discovered as a possible management issue. Minor mortality at such facilities also was reported for eastern small-footed myotis, cave myotis, long-legged myotis, and big free-tailed bats in the U.S.

Research findings relevant to management concerns for eastern forest species of concern have most intensively concentrated on Rafinesque's big-eared bats in bottomland hardwood forests, where natural roosts are in hollow trees (more frequently in live trees rather than snags). Management practices that retain and recruit large trees with large internal cavities in flooded areas are thought to be critical for maintaining roosting populations of this species, with more specific recommendations regarding appropriate tree species made in different regions. In many areas, protection of roosts and surrounding habitat was recommended for colonies in human-made structures such as old buildings, bridges, wells and cisterns. Rafinesque's big-eared bats can adapt roosting habits to use human-made structures (cinder-block towers, culverts) that mimic natural roosts and hollow trees with openings created by managers. Southeastern myotis at the southern part of their distribution require protection of caves used by maternity colonies, and a growing number of these sites are being protected by gates, perimeter fencing, or access restrictions. In states other than Florida, the southeastern myotis may rely more heavily on hollow trees in bottomland hardwood forests. Conservation of such habitats, including tracts with large hollow trees of species and configurations known to be used as roosts by southeastern myotis, will be of benefit to populations of this bat. The recent findings that the eastern small-footed myotis roosts in talus or talus-like areas may warrant more attention for future management. The extent to which populations of eastern small-footed myotis have suffered from white-nose syndrome is not accurately known, but these roosting habits may bear upon their susceptibility to this disease.

Two of three species of bats in the southwestern arid lowlands have not been intensively studied with aims toward management. Loss of riparian habitat is thought to be the greatest issue of concern for the Mexican long-tongued bat, and maintenance of water sources with adequate surface areas known to be relied on for drinking appears to be critical for Underwood's bonneted bats. California leaf-nosed bats have suffered from loss of roosting and foraging habitat. Bat-compatible closure methods at abandoned mines occupied by this species have been successful at selected sites, but careful planning is required because some methods have not been successful in other instances. Loss of habitat due to agricultural conversion, encroachment by people, and disturbance are issues for conservation of California leaf-nosed bats, with preservation of remaining desert washes for foraging a conservation priority. California leaf-nosed bats will respond positively to provision of artificial water sources.

The three species considered to be characteristic of western uplands with cliffs and canyons also have been little studied from the standpoint of management for conservation. Spotted bats and big free-tailed bats rely on earthen ponds constructed for livestock as sources of water in some regions, and maintenance of earthen ponds during times of drought has been recommended. Maintenance of larger-sized ponds may be especially critical for big free-tailed bats and greater bonneted bats. Mining and quarrying at cliffs, road construction through cliff-walled canyons, disturbance from recreational climbing, and submergence by large water impoundments have been noted as having potential impacts on colonies of these cliff-dwelling bats.

Roost use and roosting habitat have been topics of much study in bats of western coniferous forests and woodlands. Several general recommendations for forest management in dry ponderosa pine forests include retaining in place patches of large trees that die, thinning of stands of small trees to allow faster development of larger trees, killing of live large trees in areas of low snag density to hasten roost development, and removing ground fuels from areas surrounding large snags prior to using prescribed fire. In some areas, using artificial roosts constructed to mimic exfoliating bark on snags may serve as surrogate roosts while management for developing large snags proceeds.

Recommendations for management in more moist forests such as those of the Pacific Northwest also include maintaining large-diameter conifer snags in early to intermediate stages of decay. Snags that are exposed to moderate to high levels of solar radiation (snags that protrude above the canopy, have low canopy closure, or are located in gaps or near stand edges) are most important, especially when retained in clusters, and particularly where they are in upland habitats near water. Retention of large green trees and snag creation is recommended, as is maintaining remnant patches of structurally diverse and typically older forest stands with large snags. Thinning of dense stands to accelerate development of large-diameter trees for future roosts, and creation of gaps to increase solar radiation were also recommended, as was retention of trees with large basal hollows in redwood forests. Although the full scope of hibernation sites used by western forest bats are not yet fully known, caves and mines have been documented as overwintering sites for these species. Utilization of bat-compatible closure methods to prevent disturbance at caves and mines during this critical time of year has been recommended and undertaken in several areas.

Recommendations for management of the two species generally associated with western riparian areas nested within a wider variety of broader habitats (Arizona myotis and Yuma myotis) have mostly centered on maintaining roosting habitats for maternity colonies. General recommendations made for management for roosts in trees and snags in western forest types apply where these species are found in such habitats. Minimization of disturbance around known roosting sites is important, including bat-compatible restrictions to access by people at caves and abandoned mines used by Yuma myotis. Arizona myotis appear to forage in experimentally restored cottonwood-willow riparian habitats along the lower Colorado River.

The remaining three species of concern include two species that primarily roost in caves and abandoned mines (Townsend's big-eared bat and cave myotis), and one that roosts in caves and mines but is also found roosting in snags in forests and in high cliffs (Allen's big-eared bat). Most management recommendations for cave myotis and Townsend's big-eared bats have focused on roost protection. Cave myotis are reported to be very sensitive to disturbance. In several studies colonies of cave myotis have responded well to seasonal closure of roosts and installation of bat-compatible gates, although in some areas these methods may not work well with very large colonies. Townsend's big-eared bats are also very sensitive to disturbance both in winter hibernacula and summer maternity colony sites. Restrictions to human visitation in these sites are important to avoid unintentional disturbance as well as vandalism and killing. Destruction or sealing of abandoned mines for human safety will remove roosting habitat completely, and surface mining will destroy foraging habitat. Management plans are available with details for methods to close access to these sites through use of bat-compatible gates, as summarized in the species account for the Townsend's big-eared bat. Recommendations for conservation of roosting habitat for Allen's big-eared bat are similar to those made for other cave-dwelling, snag-roosting, and cliff-roosting species.

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LITERATURE CITED

ABERNETHY, I., M. ANDERSEN, and D. KEINATH. 2013. Bats of southern Wyoming: distribution and migration. Wyoming Natural Diversity Database, Laramie, Wyoming, 90 pp. <*https://www.uwyo.edu/wyndd/_files/docs/reports/wynddreports/u12abe01wyus.pdf*>. Cited 5 September 2017.

ADAM, M.D., and J.P. HAYES. 2000. Use of bridges as night roosts by bats in the Oregon coast range. *Journal of Mammalogy* 81:402–407.

ADAMS, D.A. 1950. *Myotis subulatus leibii* in North Carolina. *Journal of Mammalogy* 31:97–98.

ADAMS, R.A., AND M.A. HAYES. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology* 77:1115–1121.

ADAMS, R.A., AND R. LAMBETH. 2015. First physical record of Allen's lappet-browed bat (*Idionycteris phyllotis*) in Colorado. *Southwestern Naturalist* 60:273–275.

ADAMS, R.A., S.C. PEDERSEN, K.M. THIBAULT, J. JADIN, AND B. PETRU. 2003. Calcium as a limiting resource to insectivorous bats: can water holes provide a supplemental mineral source? *Journal of Zoology* (*London*) 260:189–194.

AGOSTA, S.J., K.M. KUHN, AND D. MORTON. 2002. Bat night roost at an abandoned mine in western Maryland. *Canadian Field-Naturalist* 116:389–392.

AGOSTA, S.J., D. MORTON, B.D. MARSH, AND K.M. KUHN. 2005. Nightly, seasonal, and yearly patterns of bat activity at night roosts in the central Appalachians. *Journal of Mammalogy* 86:1210–1219.

ALABAMA DEPARTMENT OF CONSERVATION AND NATURAL RESOURCES. 2005. Conserving Alabama's wildlife: a comprehensive strategy. 339 pp. <*http://www.teaming.com/sites/default/files/Alabama%20Wildlife%20Action%20Plan.pdf*>. Cited 5 September 2017.

ALABAMA DEPARTMENT OF CONSERVATION AND NATURAL RESOURCES. 2015a. Bats. <*http://www.outdooralaba-*

ma.com/Bats/>. Cited 5 September 2017.

Alabama Department of Conservation and Natural Resources. 2015b. Alabama Wildlife Action Plan 2015–2025. 523 pp. <*http://www.outdooralabama.com/sites/default/files/AL-SWAP-DRAFT-30JULY_0.pdf*>. Cited 5 September 2017.

Alabama Department of Conservation and Natural Resources. 2017. Survey finds first southeastern bat with white-nose syndrome. Alabama Department of Conservation and Natural Resources Press Release. <*http://www.outdooralabama.com/survey-finds-first-southeastern-bat-white-nose-syndrome*>. Cited 5 September 2017.

Alaska Department of Fish and Game. 2005. Alaska's Wildlife Action Plan. <*http://www.adfg.alaska.gov/index.cfm?adfg=species.wapabout*>. Cited 5 September 2017.

Alaska Department of Fish and Game. 2015. Alaska's Wildlife Action Plan, draft for public and agency review. Alaska Department of Fish and Game Report. <*http://www.adfg.alaska.gov/static/species/wildlife_action_plan/draft_alaska_wildlife_action_plan_2015.pdf*>. Cited 5 September 2017.

Albright, R. 1959. Bat banding at Oregon Caves. *Murrelet* 40:26–27.

Alcorn, J.R. 1944. Notes on the winter occurrence of bats in Nevada. *Journal of Mammalogy* 25:308–310.

Alcorn, S.M., S.E. McGregor, and G. Olin. 1961. Pollination of saguaro cactus by doves, nectar-feeding bats, and honey bees. *Science* 133:1594–1595.

Aldridge, H. 1986. Manoeuvrability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae): *Canadian Journal of Zoology* 64:1878–1882.

Allen, G.M. 1916. Bats of the genus *Corynorhinus. Bulletin of the Museum of Comparative Zoology, Harvard College* 60:331–356.

Allen, G.M. 1919. Bats from Mount Whitney, California. *Journal of Mammalogy* 1:1–5.

Allen, G.M. 1922. Bats from New Mexico and Arizona. *Journal of Mammalogy* 3:156–162.

Allen, G.M. 1939. *Bats*. Harvard University Press, Cambridge, Massachusetts, U.S.A. 368 pp.

Allen, H. 1864. Monograph of the bats of North America. *Smithsonian Miscellaneous Collections* 165:1–85.

Allen, H. 1893. A monograph of the bats of North America. *Bulletin of the U.S. National Museum* 43:1–198.

Altenbach, J.S., and E.D. Pierson. 1995. The importance of mines to bats: an overview. Pages 7–18 *in* B.R. Riddle, ed., *Inactive Mines as Bat Habitat: Guidelines for Research, Survey, Monitoring and Mine Management in Nevada*. Proceedings from a Workshop, Reno, Nevada, January 21–22, 1994. Biological Resources Research Center, University of Nevada, Reno, Nevada.

Altenbach, J.S., and R.E. Sherwin. 2002. Importance of protecting mines. Pages 7–17 *in* K.C. Vories and D. Throgmorton, eds., *Bat Gate Design: A Technical Interactive Forum, Austin, Texas, March 4–6, 2002*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Altenbach, J.S., R. Sherwin, and P. Brown. 2000. Pre-mine closure bat survey and inventory techniques. Pages 115–125 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Alvarez-Castañeda, S.T., and M.A. Bogan. 1997. *Myotis milleri*. *Mammalian Species* (561):1–3.

Amelon, S., M. Yates, and C. Pullins. 2006. Conservation assessment: *Myotis austroriparius* (southeastern myotis) in the eastern United States. Pages 43–56 *in* Thompson, F.R., III, ed., *Conservation Assessments for Five Forest Bat Species in the Eastern United States.* U.S. Department of Agriculture, Forest Service, North Central Research Station, General Technical Report NC–260. St. Paul, Minnesota.

Ammerman, L.K., C.L. Hice, and D.J. Schmidly. 2012a. *Bats of Texas*. Texas A&M University Press, College Station, Texas. 305 pp.

Ammerman, L.K., D.N. Lee, and T.M. Tipps. 2012b. First molecular phylogenetic insights into the evolution of free-tailed bats in the subfamily Molossinae (Molossidae, Chiroptera). *Journal of Mammalogy* 93: 12–28.

Ammerman, L.K., D.N. Lee, and R.S. Pfau. 2016. Patterns of genetic divergence among *Myotis californicus*, *M. ciliolabrum*, and *M. leibii* based on amplified fragment length polymorphism. *Acta Chiropterologica* 18:337–347.

Andersen, K.W., and J.K. Jones, Jr. 1971. Mammals of northwestern South Dakota. *University of Kansas Publications, Museum of Natural History* 19:361–393.

Anderson, D.R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29:1294–1297.

Anderson, S. 1969. *Macrotus waterhousii*. *Mammalian Species* (1):1–4.

Anderson, S. 1972. Mammals of Chihuahua: taxonomy and distribution. *Bulletin of the American Museum of Natural History* 148:149–410.

Anderson, S., and C.E. Nelson. 1965. A systematic revision of *Macrotus* (Chiroptera). *American Museum of Natural History Novitates* (2212):1–39.

Annear, J. 2000. The Colorado bats/inactive mines project. Pages 233–235 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Anonymous. 1995. Courtship: bat style. *Bats* 13:16.

Anthony, H.E. 1918. The indigenous land mammals of Porto Rico, living and extinct. *Memoirs of the American Museum of Natural History* 2:333–435.

Arias-Cóyotl, E., K.E. Stoner, and A. Casas. 2006. Effectiveness of bats as pollinators of *Stenocereus stellatus* (Cactaceae) in wild, managed *in situ*, and cultivated populations in La Mixteca Baja, central Mexico. *American Journal of Botany* 93:1675–1683.

Arizaga, S., E. Ezcurra, E. Peters, F. Ramirez de Arellano, and E. Vega. 2000. Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. II. The role of pollinators. *American Journal of Botany* 87:1011–1017.

Arizona Game and Fish Department. 2011. *Myotis occultus.* Heritage Data Management System. <http://www.azgfd.gov/w_c/edits/documents/Myotoccu.fi_003.pdf>. Cited 5 September 2017.

Arizona Game and Fish Department. 2012. Arizona's State Wildlife Action Plan: 2012–2022. 245 pp. <*http://www.teaming.com/sites/default/files/Arizona%202012%20Revised.pdf*>. Cited 5 September 2017.

Arkansas Game and Fish Commission. 2014. White-nose syndrome confirmed in Marion County bats: Arkansas becomes 23rd state to confirm deadly disease in bats. Arkansas Game and Fish Commission Press Release. 2 pp. <*http://www.batcon.org/pdfs/whitenose/ArkansasWNSJan2014NewsRelease.pdf*>. Cited 5 September 2017.

Armitage, D.W., and H.K. Ober. 2012. The effects of prescribed fire on bat communities in the longleaf pine sandhills ecosystem. *Journal of Mammalogy* 93:102–114.

Armstrong, D.M., R.A. Adams, and J. Freeman. 1994. Distribution and ecology of bats of Colorado. *Natural History Inventory of Colorado, University of Colorado Museum, Boulder* 15:1–83.

Armstrong, D.M., J.P. Fitzgerald, and Meaney. 2011. *Mammals of Colorado, Second edition.* Denver Museum of Nature and Science and University Press of Colorado, Boulder, Colorado. 620 pp.

Arnett, E.B. 2007. *Presence, relative abundance, and resource selection of bats in managed forest landscapes in western Oregon*. Ph.D. dissertation. Oregon State University, Corvallis, Oregon. 223 pp.

Arnett, E.B., W.K. Brown, W.P., Erickson, J. Fiedler, B.L. Hamilton, T.H. Henry, A. Jain, G.D. Johnson, J. Kerns, R.R. Koford, C.P. Nicholson, T. O'Connell, M. Piorkowski, and R. Tankersley. 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management* 72: 61–78.

Arnett, E.B., and J.P. Hayes. 2009. Use of conifer snags as roosts by female bats in western Oregon. *Journal of Wildlife Management* 73:214–225.

Arroyo-Cabrales, J., and S.T. Álvarez-Castañeda. 2008, *Myotis leibii*. IUCN Red List of Threatened Species 2008, e.T14172A4414839. <*http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T14172A4414839.en*>. Cited 5 September 2017.

Arroyo-Cabrales, J., R.R. Hollander, and J.K. Jones, Jr. 1987. *Choeronycteris mexicana*. *Mammalian Species* (291):1–5.

Audubon, J.J., and J. Bachman. 1842. Descriptions of new species of quadrupeds inhabiting North America. *Journal of the Academy of Natural Sciences of Philadelphia* 8:280–323.

Avila-Flores, R., and M.B. Fenton. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy* 86:1193–1204.

Baerwald, E.F., and R.M.R. Barclay. 2011. Patterns of activity and fatality of migratory bats at a wind energy facility in Alberta, Canada. *Journal of Wildlife Management* 75:1003–1114.

Bagley, F., and J. Jacobs. 1984. Development of a non-intrusive population survey technique for Ozark and Virginia big-eared bat maternity colonies. *Missouri Speleology* 25:214–216.

Bailey, V. 1905. Biological survey of Texas. *North American Fauna* 25:1–222.

Bailey, V. 1931. The mammals of New Mexico. *North American Fauna* 53:1–412.

Bailey, V. 1936. The mammals and life zones of Oregon. *North American Fauna* 55:1–416.

Bain, J.R. 1981. *Roosting ecology of three Florida bats – Nycticeius humeralis, Myotis austroriparius, and Tadarida brasiliensis*. M.S. Thesis. University of Florida, Gainesville, Florida. 130 pp.

Baker, M.D., and M.J. Lacki. 2004. Forest bat communities in the East Cascade Range, Washington. *Northwest Science* 78:234–241.

Baker, M.D., and M.J. Lacki. 2006. Day-roosting habitat of female long-legged myotis in ponderosa pine forests. *Journal of Wildlife Management* 70:207–215.

Baker, R.H. 1956a. Mammals of Coahuila, Mexico. *University of Kansas Publications, Museum of Natural History* 9:125–335.

Baker, R.H. 1956b. *Eumops underwoodi sonoriensis* in Arizona. *Journal of Mammalogy* 37:111–112.

Baker, R.H., and C.J. Phillips. 1965. Mammals from El Nevado de Colima, Mexico. *Journal of Mammalogy* 46:691–693.

Balin, L. 2009. Mexican long-tongued bat (*Choeronycteris mexicana*) in El Paso, Texas. *Southwestern Naturalist* 54:225–226.

Banack, S.A. 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology* 79:1949–1967.

Banack, S.A. 2001. *Pteropus samoensis. Mammalian Species* (661):1–4.

Banack, S.A., and G.S. Grant. 2003. Reproduction and behaviour of the Samoan flying fox, *Pteropus samoensis* (Chiroptera: Pteropodidae). *Mammalia* 67:419–437.

Barbour, R.W., and W.H. Davis. 1969. *Bats of America*. The University Press of Kentucky, Lexington, Kentucky. 286 pp.

Barbour, R.W., and W.H. Davis. 1970. The status of *Myotis occultus*. *Journal of Mammalogy* 51:150–151.

Barbour, R.W., and W.H. Davis. 1974. *Mammals of Kentucky*. The University Press of Kentucky, Lexington, Kentucky. 322 pp.

Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology* 60:165–178.

Barclay, R.M.R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pages 17–59 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, eds., *Bats in Forests: Conservation and Management*. The Johns Hopkins University Press, Baltimore, Maryland.

Barclay, R.M.R., J. Ulmer, C.J.A. MacKenzie, M.S. Thompson, L. Olson, J. McCool, E. Cropley, and G. Poll. 2004. Variation in the reproductive rate of bats. *Canadian Journal of Zoology* 82:688–693.

Bassett, J.E., and J.E. Wiebers. 1979. Subspecific differences in the urine concentrating ability of *Myotis lucifugus. Journal of Mammalogy* 60:395–397.

Bayless, M.L. 2006. Designing homes for forest bats. *Bats* 26:9–11.

Bayless, M.L., M.K. Clark, R.C. Stark, B.S. Douglas, and S.M. Ginger. 2011. Distribution and status of eastern big-eared bats (*Corynorhinus* spp.). Pages 13–25 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Bell, G.P. 1985. The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Phyllostomidae). *Behavioral Ecology and Sociobiology* 16:343–347.

Bell, G.P., and M.B. Fenton. 1986. Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Animal Behavior* 34:409–414.

Bell, G.P., G.A. Bartholomew, and K.A. Nagy. 1986. The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat, *Macrotus californicus. Journal of Comparative Physiology B* 156:441–450.

Belwood, J.J. 1992. Southeastern big-eared bat. Pages 287–293 *in* Humphrey, S.R., ed., *Rare and Endangered Biota of Florida: Volume 1: Mammals*. University Press of Florida, Gainesville, Florida.

Belwood, J.J., and R.J. Waugh. 1991. Bats and mines: abandoned does not always mean empty. *Bats* 9:

13–16.

Bender, M.J., S.B. Castleberry, D.A. Miller, and T.B. Wigley. 2015. Site occupancy of foraging bats on landscapes of managed pine forest. *Forest Ecology and Management* 336:1–10.

Bennett, F.M., S.C. Loeb, M.S. Bunch, and W.W. Bowerman. 2008. Use and selection of bridges as day roosts by Rafinesque's big-eared bats. *American Midland Naturalist* 160:386–399.

Benson, S.B. 1947 Description of a mastiff bat (genus *Eumops*) from Sonora Mexico. *Proceedings of the Biological Society of Washington* 60:133–134.

Benson, S.B. 1949. The bat name *Myotis ruddi* Silliman and von Bloeker, a synonym of *Myotis volans longicrus* (True). *Journal of Mammalogy* 30:48–50.

Benson, S.B. 1954. Records of the spotted bat (*Euderma maculata*) from California and Utah. *Journal of Mammalogy* 35:117.

Berna, H.J. 1990. Seven bat species from the Kaibab Plateau, Arizona, with a new record of *Euderma maculatum. Southwestern Naturalist* 35:354–356.

Bernard, R.F., J.T. Foster, E.V. Willcox, K.L. Parise, and G.F. McCracken. 2015. Molecular detection of the causative agent of white-nose syndrome on Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and two species of migratory bats in the southeastern USA. *Journal of Wildlife Diseases* 51:519–522.

Best, T.L. 1988. Morphologic variation in the spotted bat *Euderma maculatum*. *American Midland Naturalist* 119:244–252.

Best, T.L., S.D. Carey, K.G. Caesar, and T.H. Henry. 1992. Distribution and abundance of bats (Mammalia: Chiroptera) in coastal plain caves of southern Alabama. *National Speleological Society Bulletin* 54: 61–65.

Best, T.L., and J.B. Jennings. 1997. *Myotis leibii*: *Mammalian Species* (547):1–6.

Best, T.L., W.M. Kiser, and P.W. Freeman. 1996. *Eumops perotis*. *Mammalian Species* (534):1–8.

Betts, B.J. 1997. Microclimate in Hell's Canyon mines used by maternity colonies of *Myotis yumanensis*. *Journal of Mammalogy* 78:1240–1250.

Betts, B.J. 2010. Activity budgets of Townsend's big-eared bats at a maternity colony in northeastern Oregon. *Northwestern Naturalist* 91:13–22.

Bigler, W.J., G.L. Hoff, and E.F. Ruff. 1975. Chiropteran rabies in Florida: a twenty-year analysis, 1954 to 1973. *American Journal of Tropical Medicine and Hygiene* 24:347–352.

Black, H.L. 1970. Occurrence of the Mexican big-eared bat in Utah. *Journal of Mammalogy* 51:190.

Black, H.L. 1974. A north temperate bat community: structure and prey populations. *Journal of Mammalogy* 55:138–157.

Black, H.L. 1976. American kestrel predation on the bats *Eptesicus fuscus*, *Euderma maculatum*, and *Tadarida brasiliensis*. *Southwestern Naturalist* 21:250–251.

Blanton, J.D., C.A. Hanlon, and C.E. Rupprecht. 2007. Rabies surveillance in the United States during 2006. *Journal of the American Veterinary Medical Association* 231:540–556.

Bleich, V.C., and A.M. Pauli. 1988. Additional records of the spotted bat (*Euderma maculatum*) from California. *Great Basin Naturalist* 48:563.

Bleier, W.J. 1975a. Early embryology and implantation in the California leaf-nosed bat, *Macrotus californicus*. *Anatomical Record* 182:237–254.

Bleier, W.J. 1975b. Crystalline structure in the ova and early embryological stages in a leaf-nosed bat, *Macrotus californicus*. *Journal of Mammalogy* 56:235–238.

Bodley, H.D. 1974. Ultrastructural development of the chorioallantoic placental barrier in the bat *Macrotus waterhousii. Anatomical Record* 180:351–367.

Bogan, M.A. 1974. Identification of *Myotis californicus* and *M. leibii* in southwestern North America. *Proceedings of the Biological Society of Washington* 87:49–56.

Bogan, M.A. 1999. Eastern small-footed myotis, *Myotis leibii.* Pages 93–94 *in* D.E. Wilson and S. Ruff, eds., *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, Washington, D.C.

Bogan, M.A., and P.M. Cryan. 2000. The bats of Wyoming. Pages 71–94 *in* J.R. Choate, ed., *Reflections of a Naturalist, Papers Honoring Professor Eugene H. Fleharty*. Sternberg Museum of Natural History, Fort Hays State University, Fort Hays, Kansas.

Bogan, M.A., and T.R. Mollhagen. 2016. A resurvey of bats at Dinosaur National Monument. Pages

93–125 *in* R.W. Manning, J.R. Goetze, and F.D. Yancey, II, eds., *Contributions in Natural History: A Memorial Volume in Honor of Clyde Jones*. *Special Publications of the Museum, Texas Tech University,* Lubbock, Texas.

Bogan, M.A., J.G. Osborne, and J.A. Clarke. 1996. Observations on bats at Badlands National Park, South Dakota. *Prairie Naturalist* 28:115–123.

Bogan, M.A., T.J. O'Shea, P.M. Cryan, A.M. Ditto, W.H. Shaedla, E.W. Valdez, K.T. Castle, and L.E. Ellison. 1998. *A Study of Bat Populations at Los Alamos National Laboratory and Bandelier National Monument, Jemez Mountains, New Mexico*. Los Alamos National Laboratory General Technical Report LA–UR–98–2418, Los Alamos, New Mexico. 135 pp. <*https://www.osti.gov/scitech/servlets/purl/296873–PLc0UI/webviewable/*>. Cited 5 September 2017.

Bogdanowicz, W., S. Kasper, and Owen, R.D. 1998. Phylogeny of plecotine bats: reevaluation of morphological and chromosomal data. *Journal of Mammalogy* 79:78–90.

Boland, J.L., W.P. Smith, and J.P. Hayes. 2009. Survey of bats in southeast Alaska with emphasis on Keen's myotis (*Myotis keenii*). *Northwest Science* 83:169–179.

Bonaccorso, F., K. Helgen, A. Allison, and G. Wiles. 2008. *Pteropus tokudae*. IUCN Red List of Threatened Species. e.T18763A8585073. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T18763A8585073.en >. Cited 1 December 2017.

Bonilla, C., E. Cisneros, and V. Sánchez-Cordero. 1992. First record of the Mexican big-eared bat *Idionycteris phyllotis* (Vespertilionidae) in the State of Oaxaca, México. *Southwestern Naturalist* 37:429–430.

Borell, A.E. 1939. A colony of rare free-tailed bats. *Journal of Mammalogy* 20:65–68.

Boutin, M.J., and C.K.R. Willis. 1996. A new longevity record for *Myotis yumanensis*. *Bat Research News* 37:11.

Bowen, R.A., T.J. O'Shea, V. Shankar, M.A. Neubaum, D.J. Neubaum, and C.E. Rupprecht. 2013. Prevalence of neutralizing antibodies to rabies virus in serum of seven species of insectivorous bats from Colorado and New Mexico, United States. *Journal of Wildlife Diseases* 49:367–374.

Bowles, J.B. 1975. Distribution and biogeography of mammals of Iowa. *Special Publications of the Museum, Texas Tech University* 9:1–184.

Boyles, J.G., P.M. Cryan, G.F. McCracken, and T.H. Kunz. 2011. Economic importance of bats in agriculture. *Science* 332:41–42.

Boyles, J.G., M.B. Dumbar, and J.O. Whitaker, Jr. 2006. Activity following arousal in winter in North American vespertilionid bats. *Mammal Review* 36:267–280.

Bradley, R.D., L.K. Ammerman, R.J. Baker, L.C. Bradley, J.A. Cook, R.C. Dowler, C. Jones, D.J. Schmidly, F.B. Stangl, Jr., R.A. Van Den Bussche, and B. Würsig. 2014. Revised checklist of North American mammals north of Mexico, 2014. *Occasional Papers, Museum of Texas Tech University* 327:1–27.

Bradley, W.G., and R.A. Mauer. 1965. A collection of bats from Chihuahua, Mexico. *Southwestern Naturalist* 10:74–75.

Bradley, W.G., and M.J. O'Farrell. 1967. The mastiff bat, *Eumops perotis*, in southern Nevada. *Journal of Mammalogy* 48:672.

Bradshaw, G.V.R. 1961. *A life history study of the California leaf-nosed bat, Macrotus californicus*. Ph.D. Dissertation. University of Arizona, Tucson, Arizona. 89 pp.

Bradshaw, G.V.R. 1962. Reproductive cycle of the California leaf-nosed bat, *Macrotus californicus*. *Science* 136:645–646.

Bradshaw, G.V.R., and B. Hayward. 1960. Mammal skulls recovered from owl pellets in Sonora, Mexico. *Journal of Mammalogy* 41:282–233.

Braun, J.K., B. Yang, S.B. González–Pérez, and M.A. Mares. 2015. *Myotis yumanensis*. *Mammalian Species* (47):1–14.

Brennan, R.E., Jr., W. Caire, N. Pugh, S. Chapman, A.H. Robbins, and D.E. Akiyoshi. 2015. Examination of bats in western Oklahoma for antibodies against *Pseudogymnoascus destructans*, the causative agent of white–nose syndrome. *Southwestern Naturalist* 60:45–150.

Brigham, R.M., H.D.J.N. Aldridge, and R.L. Mackey. 1992. Variation in habitat use and prey selection by

Yuma bats, *Myotis yumanensis*. *Journal of Mammalogy* 73:640–645.

Brooke, A. 1997, Fruit bat studies: *Pteropus samoensis* and *Pteropus tonganus* 1995–1996. Department of Marine and Wildlife Resources, Management Biological Report, Pago Pago, American Samoa. 64 pp <*http://www.botany.hawaii.edu/basch/uhnpscesu/pdfs/sam/Brooke1997abat95a96AS.pdf*>. Cited 5 September 2017.

Brooke, A.P. 2001. Population status and behaviours of the Samoan flying fox (*Pteropus samoensis*) on Tutuila Island, American Samoa. *Journal of Zoology* (*London*) 254:309–319.

Brooke, A.P., C. Solek, and A. Tualaulelei. 2000. Roosting behavior of colonial and solitary flying foxes in American Samoa (Chiroptera: Pteropodidae). *Biotropica* 32:338–350.

Brown, P.E. 1995. Impacts of renewed mining in historic districts and mitigation for impacts on bat populations. Pages 138–140 *in* B.R. Riddle, ed., *Inactive Mines as Bat Habitat: Guidelines for Research, Survey, Monitoring and Mine Management in Nevada*. Proceedings from a Workshop, Reno, Nevada, January 21–22, 1994. Biological Resources Research Center, University of Nevada, Reno, Nevada.

Brown, P.E. 2006. Lower Colorado River bat monitoring protocol. U.S. Bureau of Reclamation, Lower Colorado River Multi–Species Conservation Program, Boulder City, Nevada. 27 pp. <*https://www.lcrmscp.gov/reports/2006/f4_bat_mon_protocol_jan06.pdf*>. Cited 21 September 2017.

Brown, P.E. 2013. Roost surveys and monitoring for Lower Colorado River bat species 2013 annual report. U.S. Bureau of Reclamation, Lower Colorado River Multi–Species Conservation Program, Boulder City, Nevada. 52 pp. <*https://www.lcrmscp.gov/reports/2013/d9_annrep_roost_2013.pdf*>. Cited 5 September 2017.

Brown, P.E., and Berry, R.D. 1991. Bats: habitat, impacts and mitigation. Pages 26–30 *in Issues and Technology in the Management of Impacted Wildlife, Snowmass, Colorado, April 8–10, 1991, Proceedings*. Thorne Ecological Institute, Snowmass, Colorado.

Brown, P.E., and R.D. Berry. 1999. Bat survey of the Hualapai Mountains. Arizona Game and Fish Department Heritage Report Fiscal Years 1997–1998, Phoenix, Arizona. 17 pp. <*http://azmemory.azlibrary.gov/cdm/ref/collection/statepubs/id/16698*>. Cited 5 September 2017.

Brown, P.E., and R.D. Berry. 2005. *Bat surveys and the development of monitoring protocol for Santa Monica Mountains National Recreation Area*. Final Report Agreement # H8548020024. Santa Monica Mountains National Recreation Area, National Park Service, Thousand Oaks, California. 35 pp.

Brown, P.E., R.D. Berry, and C. Brown. 1993a. Bats and mines: finding solutions. *Bats* 11:12–13.

Brown, P.E., R.D. Berry, and C. Brown. 1993b. The California leaf-nosed bat (*Macrotus californicus*) in the California desert. *San Bernardino County Museum Association Quarterly* 40:23.

Brown, P.E., R.D. Berry, and C. Brown. 1994. Foraging behavior of Townsend's big-eared bats (*Plecotus townsendii*) on Santa Cruz Island, Pages 367–370 *in* W.L. Halvorson and G.J. Maender, eds., *The Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, California.

Buecher, D., and B. Buecher. 2002. Bat roost protection: closure design using soft closures. Pages 97–101 *in* K.C. Vories and D. Throgmorton, eds., *Bat Gate Design: A Technical Interactive Forum, Austin, Texas, March 4–6, 2002*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Bureau of Land Management. 2008. Manual transmittal sheet 6840 special status species management. U.S. Department of Interior Bureau of Land Management Form 1221–2. 48 pp. <*https://www.nrc.gov/docs/ML1223/ML12237A217.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2009a. BLM Colorado state director's sensitive species list. U.S. Department of Interior Bureau of Land Management Report, Lakewood, Colorado. 6 pp. <https://web.archive.org/web/20170312114150/<*http://www.blm.gov/style/medialib/blm/co/programs/botany.Par.8609.File.dat/BLM%20CO%20SD%20Sensitive%20Spec.%20List.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2009b. Montana/Dakotas special status species list. U.S. Department of Interior Bureau of Land Management Report, Billings, Montana. 7 pp. <*https://eplanning.blm.gov/epl-front-office/projects/lup/38214/46419/50130/Preparation_Plan_for_Lewistown_RMP__Appendix_3_(508_Compliant).pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2010a. Special status animals in California, including BLM designated sensitive species. U.S. Department of Interior Bureau of Land Management Report, Sacramento, California. 3 pp. <*https://www.blm.gov/ca/dir/pdfs/2010/im/CAIM2010–008ATT1.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2010b. BLM Wyoming sensitive species policy and list. U.S. Department of Interior Bureau of Land Management Report, Cheyenne, Wyoming. 14 pp. <*http://www.swccd.us/docs/M_WyoBLM_Sensitivespecies.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2010c. Utah BLM sensitive fish and wildlife species list. Department of Interior Bureau of Land Management Report, Salt Lake City, Utah. 2 pp. <*https://www.blm.gov/programs/fish-and-wildlife/threatened-and-endangered/state-te-data/utah*>. Cited 5 September 2017.

Bureau of Land Management. 2011a. New Mexico BLM sensitive animal species list (final). U.S. Department of Interior, Bureau of Land Management Report, Santa Fe, New Mexico. 26 pp. <*https://www.blm.gov/sites/blm.gov/files/documents/files/Programs_FishandWildlife_BLMNM%20Special%20Status%20Species.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2011b. Updated Bureau of Land Management (BLM) sensitive species list for Nevada. U.S. Department of Interior Bureau of Land Management Report, Reno, Nevada. 4 pp. <*https://www.blm.gov/download/file/fid/12688*>. Cited 5 September 2017.

Bureau of Land Management. 2015a. Idaho special status animal species: type 2. U.S. Department of Interior Bureau of Land Management Report, Boise, Idaho. 12 pp. <*https://www.blm.gov/download/file/fid/12084*>. Cited 5 September 2017.

Bureau of Land Management. 2015b. Final OR/WA state director special status species list. U.S. Department of Interior Bureau of Land Management Report, Portland, Oregon. 60 pp. <*https://www.blm.gov/or/efoia/fy2008/im/p/im-or-2008–038.pdf*>. Cited 5 September 2017.

Bureau of Land Management. 2017. Arizona Bureau of Land Management sensitive species list. U.S. Department of Interior Bureau of Land Management Form 1221–2, Phoenix, Arizona. 6 pp. <*https://www.blm.gov/policy/az-im-2017–009*>. Cited 5 September 2017.

Burford, L.S., and M.J. Lacki. 1998. Moths consumed by *Corynorhinus townsendii virginianus* in eastern Kentucky. *American Midland Naturalist* 139:141–146.

Burghardt, J.E. 2000. Bat-compatible closures of abandoned underground mines in National Park system units. Pages 79–98 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Burt, W.H. 1934. The mammals of southern Nevada. *Transactions of the San Diego Society of Natural History* 7:375–427.

Cain, G.D. 1966. Helminth parasites of bats from Carlsbad Caverns, New Mexico. *Journal of Parasitology* 52:351–357.

Cain, G.D., and E.H. Studier. 1974. Parasitic helminths of bats from the southwestern United States and Mexico. *Proceedings of the Helminthological Society of Washington* 41:113–114.

Caire, W., and L.S. Loucks. 2010. Loss in mass by hibernating cave myotis, *Myotis velifer* (Chiroptera: Vespertilionidae) in western Oklahoma. *Southwestern Naturalist* 55:323–330.

Caire, W., and L. Loucks. 2013. The greater mastiff bat *Eumops perotis* (Chiroptera: Molossidae) in Oklahoma. *Southwestern Naturalist* 58:102–104.

Caire, W., L.S. Loucks, and P.L. Brown. 2014. Bat rabies in Oklahoma. *Southwestern Naturalist* 59: 548-553.

Caire, W., J.F. Smith, S. McGuire, and M.A. Royce. 1984. Early foraging behavior of insectivorous bats in western Oklahoma. *Journal of Mammalogy* 65:319–324.

California Department of Fish and Wildlife. 2015a. State and federally listed endangered and threatened animals of California. 14 pp. <*https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=109405&inline=1*>. Cited 5 September 2017.

California Department of Fish and Wildlife. 2015b. California state wildlife action plan 2015 update: a conservation legacy for Californians. Sacramento, California. 804 pp. <*https://www.wildlife.ca.gov/SWAP/Final*>. Cited 5 September 2017.

California Department of Fish and Wildlife. 2017. Natural diversity database, special animals list. California Department of Fish and Wildlife Periodic Publication, Sacramento, California. 65 pp.

<*https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=109406&inline=1*>. Cited 5 September 2017.

CALVERT, A.W., AND S.A. NEISWENTER. 2012. Bats in riparian-restoration sites along the lower Colorado River, Arizona. *Southwestern Naturalist* 57:340–342.

CAMPBELL, B. 1934. Notes on bats collected in Arizona during the summer of 1933. *Journal of Mammalogy* 15:241–242.

CAROTHERS, S.W., AND G.A. RUFFNER. 1974. Notes on *Tadarida macrotis* in northwestern Arizona. *Southwestern Naturalist* 15:395.

CARPENTER, G.M., E.V. WILLCOX, R.F. BERNARD, AND W.H. STIVER. 2016. Detection of *Pseudogymnoascus destructans* on free-flying male bats captured during summer in the southeastern USA. *Journal of Wildlife Diseases* 52:922–926.

CARRAWAY, L.N. 2009. Comments on "field identification of *Myotis yumanensis* and *Myotis lucifugus*: a morphological evaluation". *Western North American Naturalist* 69:277–278.

CARSTENS, B.C., AND T.A. DEWEY. 2010. Species delimitation using a combined coalescent and information-theoretic approach: an example from North American Myotis bats. *Systematic Zoology* 59:400–414.

CARTER, D.C., R.H. PINE, AND W.B. DAVIS. 1966. Notes on Middle American bats. *Southwestern Naturalist* 11:488–499.

CARVER, B.D., AND N. ASHLEY. 2008. Roost tree use by sympatric Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*). *American Midland Naturalist* 160: 364–373.

CARY, M. 1911. A biological survey of Colorado. *North American Fauna* 33:1–256.

CASTNER, S.V., T.K. SNOW, AND D.C. NOEL. 1995. Bat inventory of the Imperial National Wildlife Refuge. Arizona Game and Fish Department Technical Report 70, Phoenix, Arizona. 30 pp. <*http://www.azgfd.gov/w_c/documents/NGTR070.pdf*>. Cited 5 September 2017.

CENTER FOR BIOLOGICAL DIVERSITY. 2010. Petition to list the eastern small-footed bat *Myotis leibii* and northern long-eared bat *Myotis septentrionalis* as threatened or endangered under the Endangered Species Act. Center for Biological Diversity, Richmond, Vermont. 61 pp. <*https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&cad=rja&uact=8&ved=0ahUKEwiThKCF4pHWAhVByoMKHRXXBTQQFggmMAA&url=<http%3A%2F%2Fwww.biological-diversity.org%2Fcampaigns%2Fbat_crisis_white-nose_syndrome%2Fpdfs%2Fpetition-Myotisleibii-Myotisseptentrionalis.pdf&usg=AFQjCNFRHPYSQH0czTVnvPS0STPQwhpuFQ*>. Cited 5 September 2017.

CHAMBERS, C.L., V. ALM, M.S. SIDERS, AND M.J. RABE. 2002. Use of artificial roosts by forest-dwelling bats in northern Arizona. *Wildlife Society Bulletin* 30:1085–1091.

CHAMBERS, C.L., M.J. HERDER, K. YASUDA, D.G. MIKESIC, S.M. DEWHURST, W.M. MASTERS, AND D. VLECK. 2011. Roosts and home ranges of spotted bats (*Euderma maculatum*) in northern Arizona. *Canadian Journal of Zoology* 89:1256–1267.

CHAMBERS, C.L., C.D. VOJTA, E.D. MERING, AND B. DAVENPORT. 2015. Efficacy of scent-detection dogs for locating bat roosts in trees and snags. *Wildlife Society Bulletin* 39:780–787.

CHAPMAN, S.S., AND B.R. CHAPMAN. 1990. Bats from the coastal region of southern Texas. *Texas Journal of Science* 42:13–22.

CHOATE, J.R., AND J.M. ANDERSON. 1997. Bats of Jewel Cave National Monument, South Dakota. *Prairie Naturalist* 29:39–47.

CHRUSZCZ, B.J., AND R.M.R. BARCLAY. 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Functional Ecology* 16:18–26.

CHRUSZCZ, B.J., AND R.M.R. BARCLAY. 2003. Prolonged foraging bouts of a solitary gleaning/hawking bat, *Myotis evotis*. *Canadian Journal of Zoology* 81:823–826.

CHUNG–MACCOUBREY, A.L. 1996. Bat species composition and roost use in pinyon-juniper woodlands of New Mexico. Pages118–123 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

CHUNG-MACCOUBREY, A. 1999. Maternity roosts of bats at the Bosque del Apache National Wildlife Refuge: A preliminary report. Pages 187–190 *in* D.M. Finch, J.C. Whitney, J.F. Kelley, and S.R. Loftin, eds., *Rio*

Grande Ecosystems: Linking Land, Water, and People Toward a Sustainable Future for the Middle Rio Grande Basin, June 2–5, 1998. USDA Forest Service Proceedings, RMRS–P–7, Albuquerque, New Mexico.

Chung-MacCoubrey, A.L. 2003. Monitoring long-term reuse of trees by bats in pinyon-juniper woodlands of New Mexico. *Wildlife Society Bulletin* 31:1–7.

Chung-MacCoubrey, A. 2005. Use of pinyon-juniper woodlands by bats in New Mexico. *Forest Ecology and Management* 204:209–220.

Chung-MacCoubrey, A., and M.A. Bogan. 2003. Bats of the piñon-juniper woodlands of southwestern Colorado. Pages 131–149 *in* M.L. Floyd, ed., *Ancient Piñon-Juniper Woodlands: A Natural History of Mesa Verde Country.* University Presses of Colorado, Boulder, Colorado.

Clark, D.R., Jr. 1991. Bats, cyanide, and gold mining. *Bats* 9:17–18.

Clark, D.R., Jr., and R.L. Hothem. 1991. Mammal mortality at Arizona, California, and Nevada gold mines using cyanide extraction. *California Fish and Game* 77:61–69.

Clark, D.R., Jr., A.S. Wenner, and J.F. Moore. 1986. Metal residues in bat colonies, Jackson County, Florida, 1981–1983. *Florida Field Naturalist* 14:38–45.

Clark, M.K. 1990. *Roosting ecology of the eastern big-eared bat, Plecotus rafinesquii, in North Carolina*. M.S. Thesis. North Carolina State University. 112 pp.

Clark, M.K. 2003. Survey and monitoring of rare bats in bottomland hardwood forests. Pages 79–90 *in* T.J. O'Shea and M.A. Bogan, eds., *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*. U.S. Geological Survey Information Technology Report ITR 2003–003.

Clark, M.K., D.S. Lee, and J.B. Funderburg, Jr. 1985. The mammal fauna of Carolina bays, pocosins and associated communities in North Carolina: an overview. *Brimleyana* 11:1–38.

Clement, M.J., and Castleberry, S.B. 2011. Comparison of survey methods for Rafinesque's big-eared bats. Pages 147–157 *in* S.C. Loeb, M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Clement, M.J., and Castleberry, S.B., 2013a, Southeastern myotis (*Myotis austroriparius*) roost selection in cypress-gum swamps. *Acta Chiropterologica* 15:133–141.

Clement, M.J., and Castleberry, S.B. 2013b. Divergent roosting habits of Rafinesque's big-eared bat and southeastern myotis during winter floods. *American Midland Naturalist* 170:158–170.

Clement, M.J., and Castleberry, S.B. 2013c. Summer tree roost selection by Rafinesque's big-eared bat. *Journal of Wildlife Management* 77:414–422.

Clement, M.J., and Castleberry, S.B. 2013d. Estimating density of a forest-dwelling bat: a predictive model for Rafinesque's big-eared bat. *Population Ecology* 55:205–215.

Cockrum, E.L. 1952. Mammals of Kansas. *University of Kansas Publications, Museum of Natural History* 7:1–303.

Cockrum, E.L. 1955. Reproduction in North American bats. *Transactions of the Kansas Academy of Science* 58:487–511.

Cockrum, E.L. 1956. New genus and species, *Idionycteris phyllotis*, recorded from the United States. *Journal of Mammalogy* 37:546–547.

Cockrum, E.L. 1960. Distribution, habitat and habits of the mastiff bat, *Eumops perotis*, in North America. *Journal of the Arizona Academy of Science* 1:79–84.

Cockrum, E.L. 1969. Insecticides and Arizona bat populations. *Journal of the Arizona Academy of Science* 5:198.

Cockrum, E.L. 1970. Insecticides and guano bats. *Ecology* 51:761–762.

Cockrum, E.L., 1973, Additional longevity records for American bats. *Journal of the Arizona Academy of Sciences* 8:108–110.

Cockrum, E.L., and B.F. Musgrove. 1964a. Additional records of the Mexican big-eared bat, *Plecotus phyllotis* (Allen), from Arizona. *Journal of Mammalogy* 45:472–474.

Cockrum, E.L., and B. Musgrove. 1964b. Cave myotis, *Myotis velifer*, from southern Nevada. *Journal of Mammalogy* 45:636–637.

Cockrum, E.L., B. Musgrove, and Y. Petryszyn. 1996. Bats of Mohave County, Arizona: populations and movements. *Occasional Papers, The Museum Texas Tech University* 157:1–72.

Cockrum, E.L., and A. Gardner. 1960. Underwood's mastiff bat in Arizona. *Journal of Mammalogy* 41: 510–511.

Cockrum, E.L., and E. Ordway. 1959. Bats of the Chiricahua Mountains, Cochise County, Arizona. *American Museum Novitates* (1938):1–35.

Coleman, J.L., and R.M.R. Barclay. 2012. Urbanization and the abundance and diversity of prairie bats. *Urban Ecosystems* 15:87–102.

Coleman, J.T.H., and J.D. Reichard. 2014. Bat white-nose syndrome in 2014: a brief assessment seven years after discovery of a virulent fungal pathogen in North America. *Outlooks on Pest Management* 25: 374–377.

Coleman, L.S., W.M. Ford, C.A. Dobony, and E.R. Britzke. 2014. A comparison of passive and active acoustic sampling for a bat community impacted by white-nose syndrome. *Journal of Fish and Wildlife Management* 5:217–226.

Colorado Parks and Wildlife. 2015a. Threatened and endangered list. <*http://cpw.state.co.us/learn/Pages/SOC–ThreatenedEndangeredList.aspx*>. Cited 5 September 2017.

Colorado Parks and Wildlife. 2015b. Colorado's 2015 state wildlife action plan. 865 pp. <*http://cpw.state.co.us/aboutus/Pages/StateWildlifeActionPlan.aspx*>. Cited 5 September 2017.

Comer, C.E., L.A. Stuemke, M.L. Morrison, and R.W. Maxey. 2014. Comparison of systematic roost searches and acoustic detection to determine occupancy of rare forest bats. *Wildlife Society Bulletin* 38:103–110.

Commissaris, L.R. 1959. Notes on the Yuma myotis in New Mexico. *Journal of Mammalogy* 40:441–442.

Commissaris, L.R. 1961. The Mexican big-eared bat in Arizona. *Journal of Mammalogy* 42:61–65.

Connecticut Department of Energy and Environmental Protection. 2015. Connecticut's Wildlife Action Plan 2015 Revision. 561 pp. <*http://www.ct.gov/deep/cwp/view.asp?a=2723&q=329520&deepNav_GID=1719#Review*>. Cited 5 September 2017.

Constantine, D.G. 1961a. Locality records and notes on western bats. *Journal of Mammalogy* 42:404–405.

Constantine, D.G. 1961b. Spotted bat and big free-tailed bat in northern New Mexico. *Southwestern Naturalist* 6:92–97.

Constantine, D.G. 1967. Bat rabies in the southwestern United States. *Public Health Reports* 82:867–888.

Constantine, D.G. 1979. An updated list of rabies-infected bats in North America. *Journal of Wildlife Diseases* 15:347–349.

Constantine, D.G. 1987. Long-tongued bat and spotted bat at Las Vegas, Nevada. *Southwestern Naturalist* 32:392.

Constantine, D.G. 1988. Health precautions for bat researchers. Pages 491–528 *in* T.H. Kunz, ed., *Ecological and Behavioral Methods for the Study of Bats.* Smithsonian Institution Press, Washington, D.C.

Constantine, D.G. 1998a. Range extensions of ten species of bats in California. *Bulletin of the Southern California Academy of Science* 97:47–75.

Constantine, D.G. 1998b. An overlooked external character to differentiate *Myotis californicus* and *Myotis ciliolabrum* (Vespertilionidae). *Journal of Mammalogy* 79:624–630.

Constantine, D.G., G.L. Humphrey, and T.B. Herbenick. 1979. Rabies in *Myotis thysanodes, Lasiurus ega, Euderma maculatum*, and *Eumops perotis* in California. *Journal of Wildlife Diseases* 15:343–345.

Convention on International Trade of Wild Flora and Fauna. 2016. Appendices I, II, and III. <https://www.cites.org/eng/app/appendices.php >. Cited 5 September 2017.

Corbett, J. 2008. A strategic approach to protecting bats and mines in the Southwest. *Bats* 26:8–10.

Corbett, R.J.M., C.L. Chambers, and M.J. Herder. 2008. Roosts and activity areas of *Nyctinomops macrotis* in northern Arizona. *Acta Chiropterologica* 10:323–329.

Cortés-Calva, P., S.T. Álvarez-Castañeda, J.M. Hernández-Gutiérrez, and M. de la Paz Cuevas. 2012. Underwood's bonneted bat (*Eumops underwoodi*): first record in the Baja California Peninsula. *Western North American Naturalist* 72:412–415.

Couffer, J. 1992. *Bat Bomb, World War II's Other Secret Weapon.* University of Texas Press, Austin Texas. 252 pp.

Cox, P.A. 1983. Observations on the natural history of Samoan bats. *Mammalia* 47:519–523.

Cox, T.J. 1965. Behavior of the mastiff bat. *Journal of Mammalogy* 46:687–688.

Craig, P., and Syron, W. 1992. Fruit bats in American Samoa: their status and future. Pages 145–149 *in* D.E. Wilson and G.L. Graham, eds., *Pacific Flying Foxes: Proceedings of an International Conservation Conference.* U.S. Fish and Wildlife Service, Biological Report 90.

Craig, P., P. Trail, and T.E. Morrell. 1994. The decline of fruit bats in American Samoa due to hurricanes and overhunting. *Biological Conservation* 69:261–266.

Creecy, J.P., W. Caire, and K.A. Gilcrest. 2015. Examination of several Oklahoma bat hibernacula cave soils for *Pseudogymnoascus destructans,* the causative agent of white-nose syndrome. *Southwestern Naturalist* 60:213–217.

Crossley, D.A., Jr. and M.J. Clement. 2015. A new species of chigger (Acari: Trombiculidae) from Rafinesque's big-eared bat (Chiroptera: Vespertilionidae) in Georgia, USA. *Journal of Entomological Science* 50:248–251.

Cryan, P.M. 1997. *Distribution and roosting habits of bats in the southern Black Hills, South Dakota*. M.S. Thesis. University of New Mexico. 98 pp.

Cryan, P.M., and M.A. Bogan. 2003. Recurrence of Mexican long-tongued bats (*Choeronycteris mexicana*) at historical sites in Arizona and New Mexico. *Western North American Naturalist* 63:314–319.

Cryan, P.M., M.A. Bogan, and J.S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy* 81:719–725.

Cryan, P.M., M.A. Bogan, and G.M. Yanega. 2001. Roosting habits of four bat species in the Black Hills of South Dakota. *Acta Chiropterologica* 3:43–52.

Currie, R.R. 2000a. Federally listed threatened and endangered species of importance to mining. Pages 51–56 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Currie, R.R. 2000b. An overview of the response of bats to protection efforts. Pages 173–186 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Czaplewski, N.J. 1983. *Idionycteris phyllotis*. *Mammalian Species* (208):1–4.

Czaplewski, N.J. 1999. Long-legged myotis, *Myotis volans.* Pages 101–103 *in* D.E. Wilson and S. Ruff, eds., *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, Washington, D.C.

Dalquest, W.W. 1946. The daytime retreat of a California mastiff bat. *Journal of Mammalogy* 27:86–88.

Dalquest, W.W. 1947a. Notes on the natural history of the bat *Corynorhinus rafinesquii* in California. *Journal of Mammalogy* 28:17–30.

Dalquest, W.W. 1947b. Notes on the natural history of the bat, *Myotis yumanensis*, in California, with a description of a new race. *American Midland Naturalist* 38:224–247.

Dalquest, W.W., and M.C. Ramage.1946. Notes on the long-legged bat (*Myotis volans*) at Old Fort Tejon and Vicinity, California. *Journal of Mammalogy* 27:60–63.

Dalquest, W.W., and F.B. Stangl, Jr. 1984. The taxonomic status of *Myotis magnamolaris*, Choate and Hall. *Journal of Mammalogy* 65:485–486.

Dalquest, W.W., F.B. Stangl, Jr., and J.K. Jones, Jr. 1990. Mammalian zoogeography of a Rocky Mountain-Great Plains interface in New Mexico, Oklahoma, and Texas. *Special Publications of the Museum, Texas Tech University* 34:1–78.

Dalton, V.M., V.W. Brack, Jr., and P.M. McTeer. 1986. Food habits of the big-eared bat, *Plecotus townsendii virginianus*, in Virginia. *Virginia Journal of Science* 37:248–254.

Daschback, N. 1990. After the hurricane. *Bats* 8:14–15.

Davis, B.L., and R.J. Baker. 1974. Morphometrics, evolution, and cytotaxonomy of mainland bats of the genus *Macrotus* (Chiroptera: Phyllostomidae). *Systematic Zoology* 23:26–39.

Davis, W.B. 1974. The mammals of Texas. *Texas Parks and Wildlife Department Bulletin* 41:1–156.

Davis, W.B., and D.J. Schmidly. 1994. *The Mammals of Texas*. Texas Parks and Wildlife Press, Austin, Texas. 338 pp.

Davis, W.H. 1955. *Myotis subulatus leibii* found in unusual situations. *Journal of Mammalogy* 36:130.

Davis, W.H., and R.W. Barbour. 1970. Life history data on some southwestern *Myotis*. *Southwestern Naturalist* 15:261–273.

Davis, W.H., M.D. Hassell, and C.L. Rippy. 1965. *Myotis leibi leibi* in Kentucky. *Journal of Mammalogy* 46:683–684.

Davis, W.H., W.Z. Lidicker, Jr., and J.A. Sealander, Jr. 1955. *Myotis austroriparius* in Arkansas. *Journal of Mammalogy* 36:288.

Deacon, J.E., W.G. Bradley, and K.M. Larsen. 1964. Ecological distribution of the mammals of Clark Canyon, Charleston Mountains, Nevada. *Journal of Mammalogy* 45:397–409.

Debelica, A., A.K. Matthews, and L.K. Ammerman. 2006. Dietary study of big free-tailed bats (*Nyctinomops macrotis*) in Big Bend National Park, Texas. *Southwestern Naturalist* 51:414–418.

Debelica-Lee, A., and K.T. Wilkins. 2014. Structure and reproductive patterns in the summertime forest-bat community of southeastern Texas. *Journal of Fish and Wildlife Management* 5:413–421.

Delaware Division of Fish and Wildlife. 2006. Delaware wildlife action plan 2007–2017. 222 pp. <*http://teaming.com/sites/default/files/Delaware%20Wildlife%20Action%20Plan_0.pdf*>. Cited 5 September 2017.

Delaware Division of Fish and Wildlife. 2015. Delaware Wildlife Action Plan 2015–2025. 1,281 pp. <*http://www.dnrec.delaware.gov/fw/dwap/Documents/2015%20Submitted%20Documents/2015–2025%20DEWAP%20Entire%20Document.zip*>. Cited 5 September 2017.

Derusseau, S. N., and N.J. Huntly. 2012. Effects of gates on the nighttime use of mines by bats in northern Idaho. *Northwestern Naturalist* 93:60–66.

Dewey, T.A. 2006. *Systematics and phylogeography of North American Myotis.* Ph.D. Dissertation. University of Michigan, Ann Arbor, Michigan. 164 pp.

Diamond, G.F., and J.M. Diamond. 2014. Bats and mines: evaluating Townsend's big-eared bat (*Corynorhinus townsendii*) maternity colony behavioral response to gating. *Western North American Naturalist* 74:416–426.

Diamond, J.M., R.N. Gwinn, J. Johnson, H. Telle, and G.F. Diamond. 2015. Population characteristics of big brown bat and Arizona myotis using artificial roosting structures in northern Arizona. *Western North American Naturalist* 75:115–126.

DiSalvo, A.F., H.N. Neuhauser, and R.E. Mancke. 1992. *Nyctinomops macrotis* in South Carolina. *Bat Research News* 33:21–22.

District of Columbia Department of the Environment. 2006. District of Columbia wildlife action plan. 335 pp. <https://doee.dc.gov/SWAP2006>. Cited 5 September 2017.

District of Columbia Department of the Environment. 2015. District of Columbia Wildlife Action Plan 2015. 214 pp. <*https://doee.dc.gov/sites/default/files/dc/sites/ddoe/publication/attachments/00_2015WildLifeActionPlan_Chapters_07_31_2015_PublicVersion_0.pdf*>. Cited 5 September 2017.

Dobkin, D.S., R.D. Gettinger, and M.G. Gerdes. 1995. Springtime movements, roost use, and foraging activity of Townsend's big-eared bat (*Plecotus townsendii*) in central Oregon. *Great Basin Naturalist* 55:315–321.

Dodd, L.E., M.J. Lacki, J.S. Johnson, and L.K. Rieske. 2015. Prey size and dietary niche of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). *Southeastern Naturalist* 14:685–696.

Dolan, P.G., and D.C. Carter. 1979. Distributional notes and records for middle American Chiroptera. *Journal of Mammalogy* 60:644–649.

Dolman, R.W., and L.K. Ammerman. 2015. Molecular systematics of *Nyctinomops* (Chiroptera: Molossidae). *Western North American Naturalist* 75:43–51.

Dominguez, S.R., T.J. O'Shea, L.M. Oko, and K.V. Holmes. 2007. Detection of group 1 coronaviruses in bats in North America. *Emerging Infectious Diseases* 13:1295–1300.

Doutt, J.K., C.A. Heppenstall, and J.E. Guilday. 1966. *Mammals of Pennsylvania*. Pennsylvania Game Commission, Harrisburg, Pennsylvania. 273 pp.

Druecker, J.D. 1972. *Aspects of reproduction in Myotis volans, Lasionycteris noctivagans, and Lasiurus cinereus.* Ph.D. Dissertation, University of New Mexico, Albuquerque, New Mexico. 68 pp.

Duff, A.A., and Morrell, T.E. 2007. Predictive occurrence models for bat species in California. *Journal of*

Wildlife Management 71:693–700.

Dunnigan, P.B., and J.H. Fitch. 1967. Seasonal movements and population fluctuations of the cave bat (*Myotis velifer*) in south-central Kansas. *Transactions of the Kansas Academy of Science* 70:210–218.

Durrant, S.D. 1935. Occurrence of the spotted bat in Utah. *Journal of Mammalogy* 16:226.

Duszynski, D.W., D.T. Scott, J. Aragon, A. Leach, and T. Perry. 1999. Six new *Eimeria* species from vespertilionid bats of North America. *Journal of Parasitology* 85:496–503.

Dyke, S., S. Johnson, and P. Isakson. 2015. North Dakota State Wildlife Action Plan 2015 Draft. North Dakota Game and Fish Report. 468 pp. <*https://gf.nd.gov/wildlife/swap*>. Cited 5 September 2017.

Eads, R.B., J.S. Wiseman, and G.C. Menzies. 1957. Observations concerning the Mexican free-tailed bat, *Tadarida mexicana*, in Texas. *Texas Journal of Science* 9:277–242.

Easterla, D.A. 1965. The spotted bat in Utah. *Journal of Mammalogy* 46:665–668.

Easterla, D.A. 1970. First records of the spotted bat in Texas and notes on its natural history. *American Midland Naturalist* 83:306–308.

Easterla, D.A. 1971. Notes on young and adults of the spotted bat, *Euderma maculatum*. *Journal of Mammalogy* 52:475–476.

Easterla, D.A. 1972. A diurnal colony of big freetail bats (*Tadarida macrotis*) (Gray) in Chihuahua, Mexico. *American Midland Naturalist* 88:468–470.

Easterla, D.A. 1973. Ecology of the 18 species of Chiroptera at Big Bend National Park, Texas. *Northwest Missouri State University Studies* 34:1–165.

Easterla, D.A. 1976. Notes on the second and third newborn of the spotted bat, *Euderma maculatum*, and comments on the species in Texas. *American Midland Naturalist* 96:499–501.

Easterla, D.A., and J.O. Whitaker, Jr. 1972. Food habits of some bats from Big Bend National Park, Texas. *Journal of Mammalogy* 53:887–890.

Eger, J.L. 1977. Systematics of the genus *Eumops* (Chiroptera – Molossidae). *Life Sciences Contributions, Royal Ontario Museum* 110:1–69.

Ellinwood, S.R. 1978. *A survey of bats in southeast Colorado*. M.A. Thesis. University of Northern Colorado, Greeley, Colorado. 77 pp.

Elliott, W.E., J.E. Kaufmann, S.T. Samoray, and S.E. Gardner. 2006. The MDC method: counting bats with infrared video. Pages 147–153 *in* G.T. Rea, ed., *Proceedings of the 2005 National Cave and Karst Management Symposium, Albany, NY, Oct. 30–Nov. 4, 2005*. <*http://www.nckms.org/2005/2005.html*>. Cited 1 December 2017.

Ellis, S.E. 1993. Tabanidae as dietary items of Rafinesque's big-eared bat: implications for its foraging behavior. *Entomological News* 104:118–122.

Ellison, L.E. 2008. *Summary and Analysis of the U.S. Government Bat Banding Program*. U.S. Geological Survey Open-File Report 2008–1363, Denver, Colorado. 117 pp.

Ellison, L.E. 2010. A retrospective survival analysis of Townsend's big-eared bat (*Corynorhinus townsendii*) from Washington State. *Northwestern Naturalist* 91:172–182.

Ellison, L.E., A.L. Everette, and M.A. Bogan. 2005. Examining patterns of bat activity in Bandelier National Monument, New Mexico, by using walking point transects. *Southwestern Naturalist* 50: 197–208.

Ellison, L.E., T.J. O'Shea, M.A. Bogan, A.L. Everette, and D.M. Schneider. 2003. Existing data on colonies of bats in the United States: summary and analysis of the U.S. Geological Survey's bat population database. Pages 127–237 *in* T.J. O'Shea and M.A. Bogan, eds., *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*. U.S. Geological Survey Information Technology Report ITR 2003–003.

Enderlin, D.A. 2000. The McLaughlin mine bat program: new ideas in an old mining district. Pages 237–238 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Erickson, J.L., and S.D. West. 1996. Managed forests in the Western Cascades – the effects of seral stage on bat habitat use patterns. Pages 215–227 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

Evelyn, M.J., D.A. Stiles, and R.A. Young. 2004. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biological Conservation* 115:463–473.

Ewing, W.G., E.H. Studier, and M.J. O'Farrell. 1970. Autumn fat deposition and gross body composition in three species of *Myotis*. *Comparative Biochemistry and Physiology* 36:119–129.

Fagan, K.E., E.V. Willcox, R.F. Bernard, and W.H. Stiver. 2016. *Myotis leibii* (eastern small-footed myotis) roosting in buildings of Great Smoky Mountains National Park, Tennessee. *Southeastern Naturalist* 15:N23–N27.

Farney, J.P., and J.K. Jones, Jr. 1980. Notes on the natural history of bats from Badlands National Monument, South Dakota. *Prairie Naturalist* 12:9–12.

Faure, P.A., and Barclay, R.M.R. 1992. The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. *Animal Behaviour* 44:31–39.

Faure, P.A., and R.M.R. Barclay. 1994. Substrate–gleaning versus aerial–hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. *Journal of Comparative Physiology A* 174:651–660.

Faure, P.A., J.H. Fullard, and R.M.R. Barclay. 1990. The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *Journal of Comparative Physiology A* 166:843–849.

Feldhamer, G.A., T.C. Carter, and J.O. Whitaker, Jr. 2009. Prey consumed by eight species of insectivorous bats from southern Illinois. *American Midland Naturalist* 162:43–51.

Fellers, G.M. 2000. Predation on *Corynorhinus townsendii* by *Rattus rattus*. *Southwestern Naturalist* 45:524–527.

Fellers, G.M., and E.D. Pierson. 2002. Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. *Journal of Mammalogy* 83:167–177.

Felts, J.W., and W.D. Webster. 2003. Use of bridges as daytime roosts by bats in southeastern North Carolina. *Journal of the North Carolina Academy of Science* 119:172– 178.

Fenton, M.B. 1969. The carrying of young by females of three species of bats. *Canadian Journal of Zoology* 47:158–159.

Fenton, M.B. 1972. Distribution and overwintering of *Myotis leibii* and *Eptesicus fuscus* in Ontario. *Royal Ontario Museum Life Sciences Occasional Papers* 21:1–8.

Fenton, M.B., and G.P. Bell. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). *Canadian Journal of Zoology* 57:1271–1277.

Fenton, M.B., and G.K. Morris. 1976. Opportunistic feeding by desert bats (*Myotis* spp.). *Canadian Journal of Zoology* 54:526–530.

Fenton, M.B., and N.B. Simmons. 2015. *Bats, A World of Science and Mystery*. University of Chicago Press, Chicago, Illinois. 240 pp.

Fenton, M.B., D.C. Tennant, and J. Wyszecki. 1987. Using echolocation calls to measure the distribution of bats: the case of *Euderma maculatum*. *Journal of Mammalogy* 68:142–144.

Fenton, M.B., C.G. Van Zyll de Jong, G.P. Bell, D.B. Campbell, and M. LaPlante. 1980. Distribution, parturition dates, and feeding of bats in south-central British Columbia. *Canadian Field-Naturalist* 94:416–420.

Fernandez, M.S., A. Smith, and R. Escamilla. 2000. New county record for the Mexican long-tongued bat (*Choeronycteris mexicana*) from Texas. *Texas Journal of Science* 52:68.

Ferrara, F.J., and P.L. Leberg. 2005a. Characteristics of positions selected by day-roosting bats under bridges in Louisiana. *Journal of Mammalogy* 86:729–735.

Ferrara, F.J., and P.L. Leberg. 2005b. Influence of investigator disturbance and temporal variation on surveys of bats roosting under bridges. *Wildlife Society Bulletin* 33:1113–1122.

Findley, J.S., 1954. Reproduction in two species of *Myotis* in Jackson Hole, Wyoming. *Journal of Mammalogy* 35:434.

Findley, J.S. 1957. The hog-nosed bat in New Mexico. *Journal of Mammalogy* 38:513–514.

Findley, J.S. 1972. Phenetic relationships among bats of the genus *Myotis*. *Systematic Zoology* 21:31–52.

Findley, J.S., and C.J. Jones. 1961. New United States record of the Mexican big-eared bat. *Journal of Mammalogy* 42:97.

Findley, J.S., and C.J. Jones. 1965. Comments on spotted bats. *Journal of Mammalogy* 46:679–680.

Findley, J.S., and C.J. Jones. 1967. Taxonomic relationships of bats of the species *Myotis fortidens, M. lucifugus*, and *M. occultus*. *Journal of Mammalogy* 48:429–444.

Findley, J.S., A.H. Harris, D.E. Wilson, and C. Jones. 1975. *Mammals of New Mexico*. University of New Mexico Press, Albuquerque, New Mexico. 360 pp.

Finley, R.B., Jr., W. Caire, and D.E. Wilhelm. 1983. Bats of the Colorado oil shale region. *Great Basin Naturalist* 43:554–560.

Fitch, J.H., K.A. Shump, Jr., and A.U. Shump. 1981. *Myotis velifer*. *Mammalian Species* (149):1–5.

Flannery, T. 1995. *Mammals of the South-West Pacific and Moluccan Islands*. Cornell University Press, Ithaca, New York. 464 pp.

Fleming, H.L., J.C. Jones, J.L. Belant, and D.M. Richardson. 2013a. Multi-scale roost site selection by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) in Mississippi. *American Midland Naturalist* 169:43–55.

Fleming, H.L., J.C. Jones, J.L. Belant, and D.M. Richardson. 2013b. Probability of detection and visual count error for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) in tree cavities. *American Midland Naturalist* 169:56–65.

Fleming, T.H., T. Tibbitts, Y. Petryszyn, and V. Dalton. 2003. Current status of pollinating bats in southwestern North America. Pages 63–68 *in* T.J. O'Shea and M.A. Bogan, eds., *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*. U.S. Geological Survey Information Technology Report ITR 2003–003.

Florida Fish and Wildlife Conservation Commission. 2012. Florida's Wildlife Legacy Initiative: Florida's State Wildlife Action Plan. 662 pp. <*http://myfwc.com/conservation/special-initiatives/fwli/action-plan/*>. Cited 5 September 2017.

Fokidis, H.B., S.C. Brandebura, and T.S. Risch. 2005. Distributions of bats in bottomland hardwood forests of the Arkansas delta region. *Journal of the Arkansas Academy of Science* 59:74–79.

Foley, J., D. Clifford, K. Castle, P. Cryan, and R.S. Ostfeld. 2011. Investigating and managing the rapid emergence of white-nose syndrome, a novel, fatal, infectious disease of hibernating bats. *Conservation Biology* 25:223–231.

Ford, W.M., E.R. Britzke, C.A. Dobony, J.L. Rodrigue, and J.B. Johnson. 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. *Journal of Fish and Wildlife Management* 2:125–134.

Ford, W.M., J.M. Menzel, M.A. Menzel, J.W. Edwards, and J.C. Kilgo. 2006. Presence and absence of bats across habitat scales in the Upper Coastal Plain of South Carolina. *Journal of Wildlife Management* 70:1200–1209.

Foster, G.W., S.R. Humphrey, and P.P. Humphrey. 1978. Survival rate of young southeastern brown bats, *Myotis austroriparius*, in Florida. *Journal of Mammalogy* 59:299–304.

Fowler, A., ed. 2015. Arkansas Wildlife Action Plan. Arkansas Game and Fish Commission Report, Little Rock, Arkansas. 1678 pp. <*http://www.wildlifearkansas.com/strategy.html*>. Cited 5 September 2017.

Francl, K.E., W.M. Ford, D.W. Sparks, and V. Brack, Jr. 2012. Capture and reproductive trends in summer bat communities in West Virginia: assessing the impact of white-nose syndrome. *Journal of Fish and Wildlife Management* 3:33–42.

Freeman, G.E. 1984. *Ecomorphological analysis of an assemblage of bats: resource partitioning and competition*. Ph.D. Dissertation, University of Colorado, Boulder, Colorado. 131 pp.

Freeman, J., and R.A. Adams. 1992. Project report: conservation of Colorado's bat fauna: the effects of gating inactive mines on bat activity: Colorado Division of Wildlife processed report, Denver. 17 pp. (cited by Armstrong et al., 1994).

Freeman, P.W. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* 60:467–479.

Freeman, P.W. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. *Fieldiana Zoology*, new series 7:1–173.

Frick, W.F., J.F. Pollock, A.C. Hicks, K.E. Langwig, D.S. Reynolds, G.R. Turner, C.M. Butchkoski, and T.H. Kunz. 2010a. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682.

Frick, W.F., W.E. Rainey, and E.D. Pierson. 2007. Potential effects of environmental contamination on Yuma myotis demography and population growth. *Ecological Applications* 17:1213–1222.

Frick, W.F., D.S. Reynolds, and T.H. Kunz. 2010b. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *Journal of Animal Ecology* 79:128–136.

Fullard, J.H., and J.W. Dawson. 1997. The echolocation calls of the spotted bat *Euderma maculatum* are relatively inaudible to moths. *Journal of Experimental Biology* 200:129–137.

Galen, C., and C. Bohn. 1979. Gopher snake preys on western big-eared bat. *Murrelet* 60:27–28.

Galvão-Dias, M.A., R.M. Zancopé Oliveira, M.C. Giudice, H. Montenegro Netto, L.R. Jordão, I.M. Grigorio, A.R. Rosa, J. Amorim, J.D. Nosanchuk, L.R. Travassos, and C.P. Taborda. 2011. Isolation of *Histoplasma capsulatum* from bats in the urban area of São Paulo State, Brazil. *Epidemiology and Infection* 139:1642–1644.

Gannon, M.R. 1991. *Foraging ecology, reproductive biology, and systematics of the red fig-eating bat* (*Stenoderma rufum*) *in the tabonuco rain forest of Puerto Rico*. Ph.D. dissertation. Texas Tech University, Lubbock, Texas. 189 pp.

Gannon, M.R., and M.R. Willig. 1992. Bat reproduction in the Luquillo Experimental Forest of Puerto Rico. *Southwestern Naturalist* 37:414–419.

Gannon, M.R., and M.R. Willig. 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 26:320–331.

Gannon, M.R., and M.R. Willig. 1997. The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). *Biotropica* 29:525–529.

Gannon, M.R., M.R. Willig, and J.K. Jones, Jr. 1992. Morphometric variation, measurement error, and fluctuating asymmetry in the red fig-eating bat (*Stenoderma rufum*). *Texas Journal of Science* 44:389–404.

Gannon, M.R., A. Kurta, A. Rodríguez-Durán, and M.R. Willig. 2005. *Bats of Puerto Rico: An Island Focus and a Caribbean Perspective*. Texas Tech University Press, Lubbock, Texas. 239 pp.

Gannon, W.L., and G.R. Rácz. 2006. Character displacement and ecomorphological analysis of two long-eared *Myotis* (*M. auriculus* and *M. evotis*). *Journal of Mammalogy* 87:171–179.

Gardner, J.E., J.E. Hofmann, J.K. Krejca, J.D Garner, and S.E. Robinson. 1992. Final report: distribution and status of *Myotis austroriparius* (southeastern bat) in Illinois. Illinois Department of Conservation, Springfield, Illinois. 44 pp. <*https://www.ideals.illinois.edu/handle/2142/10051*>. Cited 5 September 2017.

Gates, J.E., G.A. Feldhamer, L.A. Griffith, and R.L. Raesly. 1984. Status of cave-dwelling bats in Maryland: importance of marginal habitats. *Wildlife Society Bulletin* 12:162–169.

Gellman, S.T., and W.J. Zielinski. 1996. Use by bats of old-growth redwood hollows on the North Coast of California. *Journal of Mammalogy* 77:255–265.

Geluso, K. 2000. Distribution of the spotted bat (*Euderma maculatum*) in Nevada, including notes on reproduction. *Southwestern Naturalist* 45:347–352.

Geluso, K. 2006. Recurrence of the spotted bat (*Euderma maculatum*) and Allen's big-eared bat (*Idionycteris phyllotis*) in New Mexico,, Final End-of-Contract Report, New Mexico Department of Game and Fish, Santa Fe, New Mexico. 34 pp, <*http://bison–m.org/documents/48618_06GelusoPub_SpottedBat_AllensBigEaredBat.pdf*>. Cited 5 September 2017.

Geluso, K. 2007. Winter activity of bats over water and along flyways in New Mexico. *Southwestern Naturalist* 52:482–492.

Geluso, K. 2008. Spotted bats (*Euderma maculatum*) from Mt. Taylor, New Mexico. *Western North American Naturalist* 68:119–122.

Geluso, K. 2017. Recurrence of the spotted bat (*Euderma maculatum*) at historical sites in New Mexico, with notes on natural history. *Occasional Papers, Museum of Texas Tech University* 346:1–14.

Geluso, K., and J.N. Mink. 2009. Use of bridges by bats (Mammalia: Chiroptera) in the Rio Grande Valley, New Mexico. *Southwestern Naturalist* 54:421–429.

Geluso, K.N. 1975. Urine concentration cycles of insectivorous bats in the laboratory. *Journal of Comparative Physiology* 99:309–319.

Geluso, K.N., and K. Geluso. 2004. Mammals of Carlsbad Caverns National Park, New Mexico. *Bulletin of the University of Nebraska State Museum* 17:1–180.

Geluso, K.N., and K. Geluso. 2012. Effects of environmental factors on capture rates of insectivorous bats, 1971–2005. *Journal of Mammalogy* 93:161–169.

Geluso, K.N., and K. Geluso. 2016. Bats of Kimball and Cheyenne counties in the panhandle of Nebraska. Pages 183–200 *in* R.W. Manning, J.R. Goetze, and F.D. Yancey, II, eds., *Contributions in Natural History: A Memorial Volume in Honor of Clyde Jones*. *Special Publications of the Museum, Texas Tech University* 65.

Geluso, K.N., and E.H. Studier. 1979. Diurnal fluctuation in urine concentration in the little brown bat, *Myotis lucifugus* in a natural roost. *Comparative Biochemistry and Physiology* 62A:471–473.

Genoways, H.H., and R.J. Baker. 1972. *Stenoderma rufum. Mammalian Species* (18):1–4.

Genoways, H.H., and J.K. Jones, Jr. 1972. Mammals from southwestern North Dakota. *Occasional Papers, Museum of Texas Tech University* 6:1–36.

Genoways, H.H., R.J. Baker, and J.E. Cornely. 1979. Mammals of the Guadalupe Mountains National Park, Texas. Pages 271–332*, in* H.H. Genoways and R.J. Baker, eds., *Biological Investigations in the Guadalupe Mountains National Park, Texas*. National Park Service, *Proceedings and Transactions Series* 4:271–332.

Genter, D.L. 1986. Wintering bats of the upper Snake River plain: occurrence in lava-tube caves. *Great Basin Naturalist* 46:241–244.

Georgia Department of Natural Resources. 2015. Revised State Wildlife Action Plan. 262 pp. <*http://georgiawildlife.com/SWAP*> Cited 5 September 2017.

Georgia Department of Natural Resources. 2016. Rare mammal species profiles. 262 pp. <*http://georgiawildlife.com/species*>. Cited 5 September 2017.

Gilley, L.M., and M.L. Kennedy. 2010. A test of mist-net configurations in capturing bats over stream corridors. *Acta Chiropterologica* 12:363–369.

Gillies, K.E., P.J. Murphy, and M.D. Matocq. 2014. Hibernacula characteristics of Townsend's big-eared bats in southeastern Idaho. *Natural Areas Journal* 34:24–30.

Glass, B.P., and R.J. Baker. 1965. *Vespertilio subulatus* Say, 1823: proposed suppression under the plenary powers (Mammalia, Chiroptera), Z.N. (S.) 1701. *Bulletin of Zoological Nomenclature* 22:204–205.

Glass, B.P., and R.J. Baker. 1968. The status of the name *Myotis subulatus* Say. *Proceedings of the Biological Society of Washington* 81:257–260.

Glass, B.P., and C.M. Ward. 1959. Bats of the genus *Myotis* from Oklahoma. *Journal of Mammalogy* 40:194–201.

Godínez-Alvarez, H., and A. Valiente-Banuet. 2000. Fruit-feeding behavior of the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds. *Biotropica* 32:552–556.

Goldman, E.A. 1914. The status of certain American species of *Myotis*. *Proceedings of the Biological Society of Washington* 27:102.

Gooding, G., and J.R. Langford. 2004. Characteristics of tree roosts of Rafinesque's big-eared bat and southeastern bat in northeastern Louisiana. *Southwestern Naturalist* 49:61–67.

Goodwin, G.C. 1940. Three new bats from Honduras and the first record of *Enchisthenes harti* (Thomas) for North America. *American Museum Novitates* (1075):1–3.

Gore, J.A., and J.A. Hovis. 1994. *Southeastern Myotis Maternity Cave Survey*. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program final performance report, Tallahassee, Florida. 33 pp.

Gore, J.A., and J.A. Hovis. 1998. Status and conservation of southeastern Myotis maternity colonies in Florida caves. *Florida Scientist* 61:160–170.

Gore, J.A., and K.R. Studenroth. 2005. Status of bats roosting in bridges in Florida. Florida Department of Transportation Research Project BD433 Final Report. 64 pp. <*http://www.fdot.gov/research/completed_proj/summary_emo/fdot_bd433_rpt.pdf* >. Cited 5 September 2017.

Gorresen, P.M., F.J. Bonaccorso, and C.A. Pinzari. 2009. Habitat occupancy and detection of the Pacific sheath-tailed bat (*Emballonura semicaudata*) on Aguiguan, Commonwealth of the Northern Mariana

Islands. *Acta Chiropterologica* 11:331–342.

Gottschalk, J.S. 1970. 50 CFR 17 Appendix D: United States list of endangered native fish and wildlife. *Federal Register* 35 (199):16047–16048.

Graham, R.E. 1966. Observations on the roosting habits of the big-eared bat, *Plecotus townsendii*, in California limestone caves. *Cave Notes: A Review of Cave and Karst Research* 8:17–22.

Grant, G.S., and S.A. Banack. 1995. Predation on *Pteropus tonganus* by a barn owl in American Samoa. *Australian Mammalogy* 18:77–78.

Grant, G.S., P. Craig, and P. Trail. 1997. Cyclone-induced shift in foraging behavior of flying foxes in American Samoa. *Biotropica* 29:224–228.

Graves, F.F., and M.J. Harvey. 1974. Distribution of Chiroptera in western Tennessee. *Journal of the Tennessee Academy of Science* 49:106–109.

Greenbaum, I.F., and R.J. Baker. 1976. Evolutionary relationships in *Macrotus* (Mammalia: Chiroptera): biochemical variation and karyology. *Systematic Zoology* 25:15–25.

Gregory, B.B., J.O. Whitaker, Jr., and G.D. Hartman. 2014. Diet of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in west-central Louisiana. *Southeastern Naturalist* 13:762–769.

Grider, J.F., A.L. Larsen, J.A. Homyack, and M.C. Kalcounis-Rueppell. 2016. Winter activity of coastal plain populations of bat species affected by white-nose syndrome and wind energy facilities. *PLoS ONE* 11: e0166512. 14 pp.

Griffin, D.R. 1940. Migrations of New England bats. *Bulletin of the Museum of Comparative Zoology at Harvard College* 86:217–246.

Griffin, D.R. 1945. Travels of banded cave bats. *Journal of Mammalogy* 26:15–23.

Grindal, S.D., T.S. Collard, R.M. Brigham, and R.M.R. Barclay. 1992. The influence of precipitation on reproduction by myotis bats in British Columbia. *American Midland Naturalist* 128:339–344.

Grinnell, A., P.E. Brown, and W.E. Rainey. 2012. The distribution and status of bats at Fort Irwin National Training Center. U.S. Army Research Office, Contract Report W911NF–10–1–0507, Research Triangle Park, North Carolina. 84 pp. <h*ttp://www.dtic.mil/docs/citations/ADA581495*>. Cited 5 September 2017.

Grinnell, H.W. 1918. A synopsis of the bats of California. *University of California Publications in Zoology* 17:223–404.

Grinnell, J. 1914. An account of the mammals and birds of the lower Colorado Valley with especial reference to the distributional problems presented. *University of California Publications in Zoology* 12: 51–294.

Grinnell, J., and H.S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California, with remarks on the behavior of geographic races on the margins of their habitats. *University of California Publications in Zoology* 10:197–406.

Gruver, J.C. 2002. *Assessment of bat community structure and roosting habitat preferences for the hoary bat* (*Lasiurus cinereus*) *near Foote Creek Rim, Wyoming*. M.S. Thesis. University of Wyoming. 149 pp.

Gunier, W.J., and W.H. Elder. 1973. New records of *Myotis leibii* from Missouri. *American Midland Naturalist* 89:489–490.

Guse, N.G., Jr. 1974. Natural accident to big free-tailed bat. *Southwestern Naturalist* 18:470.

Hackenbrack, N., M.B. Rogers, R.E. Ashley, M.K. Keel, S.V. Kubiski, J.A. Bryan, E. Ghedin, E.C Holmes, S.L. Hafenstein, and A.B. Allison. 2017. Evolution and cryo–electron microscopy capsid structure of a North American bat adenovirus and its relationship to other mastadenoviruses. *Journal of Virology* 91, UNSP e01504. 18pp.

Hagen, S.K., P.T. Isakson, and S.R. Dyke. 2005. North Dakota Comprehensive Wildlife Conservation Strategy. 454 pp. <*https://gf.nd.gov/sites/default/files/publications/north–dakota–wildlife–action–plan.pdf*>. Cited 5 September 2017.

Hall, D.B. 2000. Bat monitoring on the Nevada test site in south central Nevada. *Transactions of the Western Section of the Wildlife Society* 36:8–14.

Hall, E.R. 1935. Occurrence of the spotted bat Reno, Nevada. *Journal of Mammalogy* 16:148.

Hall, E.R. 1946. *Mammals of Nevada*. University of California Press, Berkeley. 710 pp.

Hall, E.R. 1981. *The Mammals of North America, Second Edition.* John Wiley and Sons, New York, New

York. 2 vols., 1,181 pp.

Hall, E.R., and J.W. Bee. 1960. The red fig-eating bat *Stenoderma rufum* Desmarest found alive in the West Indies. *Mammalia* 24:67–75.

Hall, E.R., and J.R. Tamsitt. 1968. A new subspecies of the red fig-eating bat from Puerto Rico. *Life Sciences Occasional Papers, Royal Ontario Museum* 11:1–5.

Hall, J.S., and F.J. Brenner. 1968. Summer netting of bats at a cave in Pennsylvania. *Journal of Mammalogy* 49:779–781.

Hamm, P.S., N.A. Caimi, D.E. Northup, E.W. Valdez, D.C. Buecher, C.A. Dunlap, D.P. Labeda, S. Lueschow, and A. Porras-Alfaro. 2017. Western bats as a reservoir of novel *Streptomyces* species with antifungal activity. *Applied Environmental Microbiology* 83:1–10. doi.org/10.1128/AEM.03057–16.

Handley, C.O., Jr. 1959. A revision of American bats of the genera *Euderma* and *Plecotus*. *Proceedings of the U.S. National Museum* 110:95–246.

Hardy, R. 1941. Some notes on Utah bats. *Journal of Mammalogy* 22:289–295.

Harris, A.H. 1974. *Myotis yumanensis* in interior southwestern North America, with comments on *Myotis lucifugus*. *Journal of Mammalogy* 55:589–607.

Harris, A.H. 1999. Yuma myotis, *Myotis yumanensis.* Pages 103–104 *in* D.E. Wilson and S. Ruff, eds., *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press Washington, D.C.

Harvey, M.J., J.R. MacGregor, and R.R. Currie. 1991. Distribution and status of Chiroptera in Kentucky and Tennessee. *Journal of the Tennessee Academy of Science* 66:191–193.

Hatfield, D.M. 1937. Notes on the behavior of the California leaf-nosed bat. *Journal of Mammalogy* 18: 6–97.

Hayes, G., and G.J. Wiles. 2013. Washington Bat Conservation Plan. Washington Department of Fish and Wildlife Report, Olympia, Washington. 138 pp.
<*http://wdfw.wa.gov/publications/01504/ wdfw01504.pdf*>. Cited 5 September 2017.

Hayes, M.A. 2011. *An analysis of fringed myotis* (*Myotis thysanodes*) *with a focus on Colorado distribution, maternity roost selection, and preliminary modeling of population dynamics*. Ph.D. dissertation. University of Northern Colorado, Greeley, Colorado. 246 pp.

Hayes, M.A., and R.A. Adams. 2014. Geographic and elevational distribution of fringed myotis (*Myotis thysanodes*) in Colorado. *Western North American Naturalist* 74:446–455.

Hayes, M.A., and R.A. Adams. 2015. Maternity roost selection by fringed myotis in Colorado. *Western North American Naturalist* 75:460–473.

Hayes, M.A., and R.A. Adams. 2017. Simulated bat populations erode when exposed to climate change projections for western North America. *PLoS ONE* 12:e0180693. 17 pp.

Hayes, M.A., K.W. Navo, L.R. Bonewell, C.J. Mosch, and R.A. Adams. 2009. Allen's big-eared bat (*Idionycteris phyllotis*) documented in Colorado based on recordings of its distinctive echolocation call. *Southwestern Naturalist* 54:499–501.

Hayes, M.A., R.A. Schorr, and K.W. Navo. 2011. Hibernacula selection by Townsend's big-eared bat in southwestern Colorado. *Journal of Wildlife Management* 75:137–143.

Haymond, S. 1998. *Summer habitat use by three vespertilionid bats in sagebrush-steppe in south east Idaho*. M.S. Thesis. Brigham Young University. 36 pp.

Hayward, B.J., 1961. *The natural history of the cave bat*, *Myotis velifer.* Ph.D. Dissertation. University of Arizona, Tucson, Arizona. 120 pp.

Hayward, B.J. 1963. A maternity colony of *Myotis occultus*. *Journal of Mammalogy* 44:279.

Hayward, B.J. 1970. The natural history of the cave bat, *Myotis velifer*. *Western New Mexico University Research in Science* 1:1–74.

Hayward, B.J., and R.R. Johnson. 1961. Notes on *Plecotus phyllotis* from Arizona. *Journal of Mammalogy* 41:402.

Heath, D.R., D.A. Saugey, and G.A. Heidt. 1986. Abandoned mine fauna of the Ouachita Mountains, Arkansas: vertebrate taxa. *Proceedings of the Arkansas Academy of Sciences* 40:33–36.

Heddergott, M., and P. Steinbach. 2015. Three new host species of *Plagiorchis micracanthos* (Macy, 1931) (Trematodes: Plagorchiidae) among North American bats (Chiroptera: Vespertilionidae). *Helminthologia*

52:155–158.

Hellebuyck, V., J.R. Tamsitt, and J.G. Hartman. 1985. Records of bats new to El Salvador. *Journal of Mammalogy* 66:783–788.

Hendricks, P. 2012. Winter records of bats in Montana. *Northwestern Naturalist* 93:154–162.

Hendricks, P., D.L. Genter, and S. Martinez. 2000. Bats of Azure Cave and the Little Rocky Mountains, Montana. *Canadian Field-Naturalist* 114:89–97.

Henny, C.J., C. Maser, J.O. Whitaker, Jr., and T.E. Kaiser. 1982. Organochlorine residues in bats after a forest spraying with DDT. *Northwest Science* 56:329–337.

Henry, S.G. 2002. Developing a project strategy. Pages 51–54 *in* K.C. Vories and D. Throgmorton, eds., *Bat Gate Design: A Technical Interactive Forum, Austin, Texas, March 4–6, 2002*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Herd, R.M. 1987. Electrophoretic divergence of *Myotis leibii* and *Myotis ciliolabrum* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 65:1857–1860.

Herd, R.M., and M.B. Fenton. 1983. An electrophoretic, morphological, and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 61:2029–2050.

Herder, M.J. 1998, Northern Arizona bat roost inventory. Arizona Game and Fish Department Heritage Fund Report I96035, Phoenix, Arizona. 27 pp. <*http://azmemory.azlibrary.gov/cdm/ref/collection/statepubs/id/16692*>. Cited 5 September 2017.

Herder, M.J., and J.G. Jackson. 2000 Roost preferences of long-legged myotis in northern Arizona. *Transactions of the Western Section of the Wildlife Society* 36:1–7.

Hermanson, J.W., and K.T. Wilkins. 1986. Pre-weaning mortality in a Florida maternity roost of *Myotis austroriparius* and *Tadarida brasiliensis*. *Journal of Mammalogy* 76:751–754.

Hevly, R.H. 1979. Dietary habits of two nectar and pollen feeding bats in southern Arizona and northern Mexico. *Journal of the Arizona-Nevada Academy of Science* 14:13–18.

Hibbard, C.W. 1934. Notes on some cave bats of Kansas. *Transactions of the Kansas Academy of Science* 37:235–238.

Higginbotham, J.L., and L.K. Ammerman. 2002. Chiropteran community structure and seasonal dynamics in Big Bend National Park. *Special Publications of the Museum, Texas Tech University* 44:1–44.

Hinck, J.E., J. Linder, A.J. Darrah, C.A. Drost, M.C. Duniway, M.J. Johnson, F.M. Méndez-Harclerode, E.M. Nowak, E.W. Valdez, C. van Riper III, and S. Wolff. 2014. Exposure pathways and biological receptors: baseline data for the Canyon Uranium Mine, Coconino County, Arizona. *Journal of Fish and Wildlife Management* 5:422–440.

Hitchcock, H.B. 1941. *Myotis subulatus leibii* and other bats hibernating in Ontario and Quebec. *Canadian Field-Naturalist* 55:46.

Hitchcock, H.B. 1945. *Myotis subulatus leibii* in Ontario. *Journal of Mammalogy* 26:433.

Hitchcock, H.B. 1949. Hibernation of bats in southeastern Ontario and adjacent Quebec. *Canadian Field Naturalist* 63:47–59.

Hitchcock, H.B. 1955. A summer colony of the least bat, *Myotis subulatus leibii* (Audubon and Bachman). *Canadian Field-Naturalist* 69:31.

Hitchcock, H.B. 1965. Twenty-three years of bat banding in Ontario and Quebec. *Canadian Field-Naturalist* 79:4–14.

Hitchcock, H.B., R. Keen, and A. Kurta. 1984. Survival rates of *Myotis leibii* and *Eptesicus fuscus* in southeastern Ontario. *Journal of Mammalogy* 65:126–130.

Hobson, C.S. 1998. *Summer distribution, status, and ecology of bats in western Virginia*. M.S. Thesis. Tennessee Technological University, Cookeville, Tennessee. 86 pp.

Hoffman, V.E., III. 1999. *Roosting and relative abundance of the southeastern myotis, Myotis austroriparius, in a bottomland hardwood forest*. M.S. Thesis. Arkansas State University, Caraway, Arkansas. 35 pp.

Hoffmann, R.S., D.L. Pattie, and J.F. Bell. 1969. The distribution of some mammals in Montana: II Bats. *Journal of Mammalogy* 50:737–741.

Hoffmeister, D.F. 1959. Distributional records of certain mammals from southern Arizona. *Southwestern Naturalist* 4:14–19.

Hoffmeister, D.F. 1970. The seasonal distribution of bats in Arizona: a case for improving mammalian range maps. *Southwestern Naturalist* 15:11–22.

Hoffmeister, D.F. 1986. *Mammals of Arizona*. University of Arizona Press, Tucson, Arizona. 602 pp.

Hoffmeister, D.F. 1989. *Mammals of Illinois*. University of Illinois Press, Urbana, Illinois. 348 pp.

Hoffmeister, D.F., and W.W. Goodpaster. 1954. The mammals of the Huachuca Mountains, southeastern Arizona. *Illinois Biological Monographs* 24:1–152.

Hoffmeister, D.F., and W.W. Goodpaster. 1962. Observations on a colony of big-eared bats, *Plecotus rafinesquii*. *Transactions of the Illinois Academy of Science* 55:87–89.

Hofmann, J.E., J.E. Gardner, J.K. Krejca, and J.D. Garner. 1999. Summer records and a maternity roost of the southeastern myotis (*Myotis austroriparius*) in Illinois. *Transactions of the Illinois State Academy of Science* 92:95–107.

Hollister, N. 1909. Two new bats from the southwestern United States. *Proceedings of the Biological Society of Washington* 22:43–44.

Holloway, G.L., and R.M.R. Barclay. 2001. *Myotis ciliolabrum*. *Mammalian Species* (670):1–5.

Host, K.M., and B. Damania. 2016. Discovery of a novel bat gammaherpesvirus. *Msphere* 1, e00016–16. 3 pp.

Howell, A.B. 1920a. Some Californian experiences with bat roosts. *Journal of Mammalogy* 1:169–177.

Howell, A.B. 1920b. Contributions to the life history of the California mastiff bat. *Journal of Mammalogy* 1:111–117.

Howell, A.B., and L. Little. 1924. Additional notes on California bats: with observations upon the young of *Eumops*. *Journal of Mammalogy* 5:261–263.

Howell, D.J. 1974. Acoustic behavior and feeding in glossophagine bats. *Journal of Mammalogy* 55: 293–308.

Huey, L.M. 1925. Food of the California leaf-nosed bat. *Journal of Mammalogy* 6:196–197.

Huey, L.M. 1932. The larger-eared free-tailed bat in San Diego. *Journal of Mammalogy* 13:160.

Huey, L.M. 1954a. *Choeronycteris mexicana* from southern California and Baja California, Mexico. *Journal of Mammalogy* 35:436–437.

Huey, L.M. 1954b. Second record of *Tadarida molossa* from San Diego, California. *Journal of Mammalogy* 35:435–436.

Humphrey, S.R. 1975. Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy* 56:321–346.

Humphrey, S.R., and J.A. Gore. 1992. Southeastern brown bat. Pages 335–342 *in* S.R. Humphrey, ed., *Rare and Endangered Biota of Florida: Volume 1: Mammals*. University Press of Florida, Gainesville, Florida.

Humphrey, S.R., and T.H. Kunz. 1976. Ecology of a Pleistocene relict, the western big-eared bat (*Plecotus townsendii*), in the southern Great Plains. *Journal of Mammalogy* 57:470–494.

Humphrey, S.R., and M.K. Oli. 2015. Population dynamics and site fidelity of the cave bat, *Myotis velifer*, in Oklahoma. *Journal of Mammalogy* 96:946–956.

Hurst, T.E., and M.J. Lacki. 1997. Food habits of Rafinesque's big-eared bat in southeastern Kentucky. *Journal of Mammalogy* 78:525–528.

Hurst, T.E., and M.J. Lacki. 1999. Roost selection, population size and habitat use by a colony of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *American Midland Naturalist* 142:363–371.

Husar, S.L. 1976. Behavioral character displacement: evidence of food partitioning in insectivorous bats. *Journal of Mammalogy* 57:331–338.

Huth, J.K., A. Silvis, P.R. Moosman, Jr., W.M. Ford, and S. Sweeten. 2015. A comparison of survey methods for documenting presence of *Myotis leibii* (eastern small-footed bats) at roosting areas in western Virginia. *Virginia Journal of Science* 66:413–425.

Idaho Department of Fish and Game. 2005. Idaho comprehensive wildlife conservation strategy. <*http://fishandgame.idaho.gov/cms/tech/CDC/cwcs.cfm*>. Cited 5 September 2017.

Idaho Department of Fish and Game. 2015. State wildlife action plan. 1,458 pp. <*https://idfg.idaho.gov/swap*>. Cited 5 September 2017.

Illinois Department of Natural Resources. 2015. Checklist of Illinois endangered and threatened animals and plants. 10 pp. <*http://www.dnr.illinois.gov/ESPB/Documents/2015_ChecklistFINAL_for_webpage_051915.pdf*>. Cited 5 September 2017.

Indiana Department of Natural Resources. 2006. Indiana Comprehensive Wildlife Strategy. 154 pp. <*http://www.in.gov/dnr/fishwild/files/CWS_MANUSCRIPT.pdf*>. Cited 5 September 2017.

Indiana Department of Natural Resources. 2015. Indiana Division of Fish and Wildlife endangered and special concern species. 2 pp. <*http://www.in.gov/dnr/fishwild/files/fw-Endangered_Species_List.pdf*>. Cited 5 September 2017.

Ingersoll, T.E., K.W. Navo, and P. de Valpine. 2010. Microclimate preferences during swarming and hibernation in the Townsend's big-eared bat, *Corynorhinus townsendii*. *Journal of Mammalogy* 91: 1242–1250.

Ingles, L.G. 1949. Hunting habits of the bat, *Myotis evotis*. *Journal of Mammalogy* 30:197–198.

Integrated Taxonomic Information System. 2017. <*https://www.itis.gov/*>. Cited 27 September 2017.

International Union for the Conservation of Nature. 2017. IUCN Red List of Threatened Species: Version 2017–1. <*http://www.iucnredlist.org/*>. Cited 5 September 2017.

Ives, R.R. 2015. *Patterns of behavior and habitat associations of Townsend's big-eared bats* (*Corynorhinus townsendii*) *in Pershing County, Nevada*. M.S. Thesis. Christopher Newport University, Newport News, Virginia. 111 pp.

Jackson, J.A., B.J. Schardien, C.D. Cooley, and B.E. Rowe. 1982. Cave myotis roosting in barn swallow nests. *Southwestern Naturalist* 27:463–464.

Jacques Whitford Stantec Ltd. 2009. Ripley Wind Power Project post-construction monitoring report. Report to Suncor Energy Products Inc. and Acciona Energy Products Inc., Calgary, Alberta. 277 pp. <*https://www.wind-watch.org/documents/ripley-wind-power-project-post-construction-monitoring-report/*>. Cited 5 September 2017.

Jagnow, D. 1998. Bat usage and cave management of Torgac Cave, New Mexico. *Journal of Cave and Karst Studies* 60:33–38.

Jameson, D.K. 1959. Survey of the parasites of five species of bats. *Southwestern Naturalist* 4:61–65.

Jennings, N.V., S. Parsons, K.E. Barlow, and M.R. Gannon. 2004. Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterologica* 6:75–90.

Jennings, W.L., and J.N. Layne. 1957. *Myotis sodalis* in Florida. *Journal of Mammalogy* 38:259.

Johnson, D.H. 1950. *Myotis subulatus leibii* in Virginia. *Journal of Mammalogy* 31:197.

Johnson, J.B., and J.E. Gates. 2007. Food habits of *Myotis leibii* during fall swarming in West Virginia. *Northeastern Naturalist* 14:317–322.

Johnson, J.B., and J.E. Gates. 2008. Spring migration and roost selection of female *Myotis leibii* in Maryland. *Northeastern Naturalist* 15:453–460.

Johnson, J.B., J.E. Gates, and W.M. Ford. 2009. Notes on foraging activity of female *Myotis leibii* in Maryland. U.S. Department of Agriculture, Forest Service, Northern Research Station Research Paper NRS–8:1–8.

Johnson, J.S., and M.J. Lacki. 2013a. Habitat associations of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and their lepidopteran prey in bottomland hardwood forests. *Canadian Journal of Zoology* 91:94–101.

Johnson, J.S., and M.J. Lacki. 2013b. Summer heterothermy in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) roosting in tree cavities in bottomland hardwood forests. *Journal of Comparative Physiology B* 183:709–721.

Johnson, J.S., and M.J. Lacki. 2013c. Effects of reproductive condition, roost microclimate, and weather patterns on summer torpor use by a vespertilionid bat. *Ecology and Evolution* 4:157–166.

Johnson, J.S., L.E. Dodd, J.D. Kiser, T.S. Peterson, and K.S. Watrous. 2012c. Food habits of *Myotis leibii* along a forested ridgetop in West Virginia. *Northeastern Naturalist* 19:665–672.

Johnson, J.S., J.D. Kiser, K.S. Watrous, and T.S. Peterson. 2011. Day-roosts of *Myotis leibii* in the Appalachian Ridge and Valley of West Virginia. *Northeastern Naturalist* 18:95–106.

Johnson, J.S., M.J. Lacki, S.C. Thomas, and J.F. Grider. 2012b. Frequent arousals from winter torpor in Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). *PLoS ONE* 7:e49754. 11 pp.

Johnson, J.S., J.N. Kropczynski, M.J. Lacki, and G.D. Langlois. 2012a. Social networks of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in bottomland hardwood forests. *Journal of Mammalogy* 93:1545–1558.

Johnson, J.S., M.J. Lacki, and M.D. Baker. 2007. Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. *Journal of Mammalogy* 88:1261–1270.

Johnson, J.S., J.J. Treanor, M.J. Lacki, M.D. Baker, G.A. Falxa, L.E. Dodd, A.G. Waag, and E.H. Lee. 2017. Migratory and winter activity of bats in Yellowstone National Park. *Journal of Mammalogy* 98:211–221.

Johnson, R.R., and J.E. Johnson. 1964. Notes on distribution of bats and other mammals in Arizona. *Journal of Mammalogy* 45:322–324.

Jones, A.K. 2016. *Mammals of the greater Gila region*. M.S. Thesis. University of New Mexico, Albuquerque, New Mexico. 219 pp.

Jones, C. 1961. Additional records of bats in New Mexico. *Journal of Mammalogy* 42:538–539.

Jones, C. 1964. *Distribution and ecology of the bats of the Mogollon Mountains area*. Ph.D. Dissertation. University of New Mexico, Albuquerque, New Mexico. 116 pp.

Jones, C. 1965. Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. *Tulane Studies in Zoology* 12:93–100.

Jones, C. 1977. *Plecotus rafinesquii*. *Mammalian Species* (69):1–4.

Jones, C., and R.W. Manning. 1989. *Myotis austroriparius*. *Mammalian Species* (332):1–3.

Jones, C., and J.F. Pagels. 1968. Notes on a population of *Pipistrellus subflavus* in southern Louisiana. *Journal of Mammalogy* 54:962–968.

Jones, C., and R.D. Suttkus. 1972. Notes on netting bats for eleven years in western New Mexico. *Southwestern Naturalist* 16:261–266.

Jones, C., and R.D. Suttkus. 1975. Notes on the natural history of *Plecotus rafinesquii*. *Occasional Papers Museum of Zoology, Louisiana State University* 47:1–14.

Jones, J.K., Jr.1963. Additional records of mammals from Durango, Mexico. *Transactions of the Kansas Academy of Science* 66:750–753.

Jones, J.K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. *University of Kansas Publications, Museum of Natural History* 16:1–356.

Jones, J.K., Jr., T. Alvarez, and M.R. Lee. 1962. Noteworthy mammals from Sinaloa, Mexico. *University of Kansas Publications, Museum of Natural History* 14:147–159.

Jones, J.K., Jr., and H.H. Genoways. 1967. A new subspecies of the fringe-tailed bat, *Myotis thysanodes*, from the Black Hills of South Dakota and Wyoming. *Journal of Mammalogy* 48:231–235.

Jones, J.K., Jr., J.R. Choate, and A. Cadena. 1972. Mammals from the Mexican state of Sinaloa: II: Chiroptera. *Occasional Papers of the Museum of Natural History, University of Kansas* 6:1–29.

Jones, J.K., Jr., H.H. Genoways, and R.J. Baker. 1971. Morphological variation in *Stenoderma rufum*. *Journal of Mammalogy* 52:244–247.

Jones, J.K., Jr., R.P. Lampe, C.A. Spenrath, and T.H. Kunz. 1973. Notes on the distribution and natural history of bats in southeastern Montana. *Occasional Papers, Museum of Texas Tech University* 15:1–12.

Jones, J.K., Jr., J.D. Smith, and T. Alvarez. 1965. Notes on bats from the Cape region of Baja California. *Transactions of the San Diego Society of Natural History* 14:53–56.

Kannan, K., S.H. Yun, R.J. Rudd, and M. Behr. 2010. High concentrations of persistent organic pollutants including PCBs, DDT, PBDEs and PFOS in little brown bats with white-nose syndrome in New York, USA. *Chemosphere* 80:613–618.

Kansas Department of Wildlife, Parks and Tourism. 2005. A future for Kansas wildlife, Kansas' comprehensive wildlife conservation strategy. 170 pp. <*http://climatechange.lta.org/wp-content/uploads/cct/2015/03/Kansas-Wildlife-Action-Plan.pdf*>. Cited 5 September 2017.

Kays, R.W., and D.E. Wilson. 2009. *Mammals of North America* (*Second Edition*). Princeton University Press, Princeton, New Jersey. 816 pp.

Kelly, R.M., J. Kitzes, H. Wilson, and A. Merenlender. 2016. Habitat diversity promotes bat activity in a vineyard landscape. *Agriculture, Ecosystems and Environment* 223:175–181.

Kendall, W. L., R.J. Barker, G.C. White, M.S. Lindberg, C.A. Langtimm, and C.L. Peñaloza. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods in Ecology and Evolution* 4:828–835.

Kendall, W.L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57:1113–1112.

Kendall, W.L., J.E. Hines, and J.D. Nichols. 2003. Adjusting multistate capture-recapture models for misclassification bias: manatee breeding proportions. *Ecology* 84:1058–1066.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.

Kentucky Department of Fish and Wildlife Resources. 2013. Kentucky's comprehensive wildlife conservation strategy. <*http://fw.ky.gov/WAP/Pages/default.aspx*>. Cited 5 September 2017.

King, K.A., A.L. Velasco, J.A. Record, and R.L. Kearns. 2001. Contaminants in bats roosting in mines at Imperial National Wildlife Refuge, Arizona, 1998–1999. U.S. Fish and Wildlife Service Project Report, Project 22410–1130–2N30, Phoenix, Arizona. 35 pp. <*https://catalog.data.gov/dataset/contaminants-in-bats-roosting-in-abandoned-mines-at-imperial-national-wildlife-refuge-1998*>. Cited 5 September 2017.

King, K.A., A.L. Velasco, C.L.H. Marr, and R.L. Kearns. 2003. Trace elements in bats roosting in mines at Kofa National Wildlife Refuge, Arizona, 2001–2002. U.S. Fish and Wildlife Service Project Report, Project 22410–1261–2N41, Phoenix, Arizona. 28 pp. <*https://catalog.data.gov/dataset/trace-elements-in-bats-roosting-in-mines-at-kofa-national-wildlife-refuge-arizona-2001–200*>. Cited 5 September 2017.

Kingston, T. 2009. Analysis of species diversity of bat assemblages. Pages 195–215 *in* T.H. Kunz and S. Parsons, eds., *Ecological and Behavioral Methods for the Study of Bats, Second Edition.* Johns Hopkins University Press, Baltimore, Maryland.

Kiser, W.M. 1995. *Eumops underwoodi*. *Mammalian Species* (516):1–4.

Klüg–Baerwald, J., C.L. Lausen, C.K.R. Willis, and R.M. Brigham. 2017. Home is where you hang your bat: winter roost selection by prairie-living big brown bats. *Journal of Mammalogy* 98:752–760.

Koford, C.B., and M.R. Koford. 1948. Breeding colonies of bats, *Pipistrellus hesperus* and *Myotis subulatus melanorhinus*. *Journal of Mammalogy* 29:417–418.

Krauel, J.J., and G. LeBuhn. 2016. Patterns of bat distribution and foraging activity in a highly urbanized temperate environment. *PLoS ONE* 11:e0168927. 18 pp.

Kretzmann, J.A. 2000. New Mexico experience with bat grates at abandoned mines. Pages 145–152 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Kretzmann, J.A. 2002. Cable nets for bat habitat preservation. Pages 103–113 *in* K.C. Vories and D. Throgmorton, eds., *Bat Gate Design: A Technical Interactive Forum, Austin, Texas, March 4–6, 2002*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Kroll, A.J., M.J. Lacki, and E.B. Arnett. 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest. *Western Journal of Applied Forestry* 27:128–136.

Krutzsch, P. 1955. Observations on the California mastiff bat. *Journal of Mammalogy* 36:407–414.

Krutzsch, P.H. 1966. Remarks on silver-haired and Leib's bats in eastern United States. *Journal of Mammalogy* 47:121.

Krutzsch, P.H. 2009. The reproductive biology of the cave myotis (*Myotis velifer*). *Acta Chiropterologica* 11:89–104.

Krutzsch, P.H., R.H. Watson, and C.D. Lox. 1976. Reproductive biology of the male leaf-nosed bat, *Macrotus waterhousii*, in southwestern United States. *Anatomical Record* 184:611–635.

Kuenzi, A.J., and M.L. Morrison. 1998. Detection of bats by mist-nets and ultrasonic sensors. *Wildlife Society Bulletin* 26:307–311.

Kuenzi, A.J., G.R. Downard, and M.L. Morrison. 1999. Bat distribution and hibernacula use in west central Nevada. *Great Basin Naturalist* 59:213–220.

Kunz, T.H. 1973. Population studies of the cave bat (*Myotis velifer*): reproduction, growth, and development. *Occasional Papers University of Kansas Museum of Natural History* 15:1–43.

Kunz, T.H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* 55:693–711.

Kunz, T.H. 1982. Roosting ecology of bats. Pages 1–55 *in* T.H. Kunz, ed., *Ecology of Bats*. Plenum Press, New York, New York.

Kunz, T.H. 2003. Censusing bats: challenges, solutions, and sampling biases. Pages 9–19 *in* T.J. O'Shea and M.A. Bogan, eds., *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*. U.S. Geological Survey Information Technology Report ITR 2003–003.

Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pages 3–89 *in* T.H. Kunz and M.B. Fenton, eds., *Bat Ecology*. University of Chicago Press, Chicago, Illinois.

Kunz, T.H., and R.A. Martin. 1982. *Plecotus townsendii*. *Mammalian Species* (175):1–6.

Kunz, T.H., M. Betke, N.I. Hristov, and M.J. Vonhof. 2009. Methods for assessing colony size, population size, and relative abundance in bats. Pages 133–157 *in* T.H. Kunz and S. Parsons, eds., *Ecological and Behavioral Methods for the Study of Bats, Second Edition.* Johns Hopkins University Press, Baltimore, Maryland.

Kurta, A. 2005. Roosting ecology and behavior of Indiana bats (*Myotis sodalis*) in summer. Pages 29–42 *in* K.C. Vories and A. Harrington, eds., *The Indiana Bat and Coal Mining*. Office of Surface Mining, U.S. Department of the Interior, Alton, Illinois.

Kwiecinski, G.G., and W.C. Coles. 2007. Presence of *Stenoderma rufum* beyond the Puerto Rican Bank. *Occasional Papers, Museum of Texas Tech University* 266:1–9.

Lack, J.B., and R.A. Van Den Bussche. 2009. A relaxed molecular clock places an evolutionary timescale on the origins of North American big-eared bats (Vespertilionidae: *Corynorhinus*). *Acta Chiropterologica* 11:15–23.

Lacki, M.J. 1996. The role of research in conserving bats in managed forests. Pages 39–48 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

Lacki, M.J., and M.D. Baker. 2007. Day roosts of female fringed myotis (*Myotis thysanodes*) in xeric forests of the Pacific Northwest. *Journal of Mammalogy* 88:967–973.

Lacki, M.J., and M. Bayless 2013. A conservation strategy for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*). Bat Conservation International, Austin, Texas. 101 pp. <*https://www.batcon.org/pdfs/ConservationPlanforCORAandMYAU_2014.pdf*>. Cited 28 November 2017.

Lacki, M.J., and L.E. Dodd. 2011. Diet and foraging behavior of *Corynorhinus* in eastern North America. Pages 39–52 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Lacki, M.J., M.D. Baker, and J.S. Johnson. 2010. Geographic variation in roost-site selection of long-legged myotis in the Pacific Northwest. *Journal of Wildlife Management* 74:1218–1228.

Lacki, M.J., M.D. Baker, and J.S. Johnson. 2012. Temporal dynamics of roost snags of long-legged myotis in the Pacific Northwest, USA. *Journal of Wildlife Management* 76:1310–1316.

Lacki, M.J., L.E. Dodd, R.S. Toomey, S.C. Thomas, Z.L. Couch, and B.S. Nichols. 2015. Temporal changes in body mass and body condition of cave-hibernating bats during staging and swarming. *Journal of Fish and Wildlife Management* 6:360–370.

Lacki, M.J., J.S. Johnson, and M.D. Baker. 2013. Temperatures beneath bark of dead trees used as roosts by *Myotis volans* in forests of the Pacific Northwest, USA. *Acta Chiropterologica* 15:143–151.

Lacki, M.J., J.S. Johnson, L.E. Dodd, and M.D. Baker. 2007. Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. *Northwest Science* 81:199–205.

Lacki, M.J., and K.M. LaDeur. 2001. Seasonal use of lepidopteran prey by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *American Midland Naturalist* 145:213–217.

Lance, R.F., and R.W. Garrett. 1997. Bat fauna of central Louisiana forests. *Texas Journal of Science* 49:181–189.

Lance, R.F., B.T. Hardcastle, A. Talley, and P.L. Leberg. 2001. Day-roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in Louisiana forests. *Journal of Mammalogy* 82:166–172.

Land, T.A. 2001. *Population size and contaminant exposure of bats using caves on Fort Hood Military Base*.

M.S. Thesis. Texas A&M University, College Station, Texas. 102 pp.

Langwig, K.E., W.F. Frick, J.T. Bried, A.C. Hicks, T.H. Kunz, and A.M. Kilpatrick. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology Letters* 15:1050–1057.

Lausen, C.L. 2005. First record of hosts for tick *Carios kelleyi* (Acari: Ixodida: Argasidae) in Canada and Montana. *Journal of Medical Entomology* 42:497–501.

Lausen, C.L. 2007. *Roosting ecology and landscape genetics of prairie bats*. Ph.D. Dissertation, University of Calgary, Calgary, Alberta, Canada. 271 pp.

Lausen, C.L., and R.M.R. Barclay. 2006. Winter bat activity in the Canadian prairies. *Canadian Journal of Zoology* 84:1079–1086.

Lausen, C.L., and T. Schowalter. 2008. Status of the western small-footed bat (*Myotis ciliolabrum*) in Alberta. Alberta Sustainable Resource Development, Wildlife Status Report Number 64. Edmonton, Alberta, Canada. 24 pp.

LaVal, R.K. 1967. Records of bats from the southeastern United States. *Journal of Mammalogy* 48:645–648.

LaVal, R.K. 1970. Infraspecific relationships of bats of the species *Myotis austroriparius. Journal of Mammalogy* 51:542–552.

LaVal, R.K. 1973. Occurrence, ecological distribution, and relative abundance of bats in McKittrick Canyon, Culberson County, Texas. *Southwestern Naturalist* 17:357–364.

LaVal, R.K., and M.L. LaVal. 1980. Ecological studies and management of Missouri bats, with emphasis on cave-dwelling species. *Missouri Department of Conservation, Terrestrial Series* 8:1–53.

Lee, D.S., and M.D. Tuttle. 1970. Old Indian Cave: Florida's first bat sanctuary. *Florida Naturalist* 44: 150–152.

Leitner, P. 1966. Body temperature, oxygen consumption, heart rate and shivering in the California mastiff bat, *Eumops perotis. Comparative Biochemistry and Physiology* 19:431–443.

Leitner, P., and S.P. Ray. 1964. Body temperature regulation of the California leaf-nosed bat, *Macrotus californicus*. *American Zoologist* 4:295.

Leonard, M.L., and M.B. Fenton. 1983. Habitat use by spotted bats (*Euderma maculatum,* Chiroptera: Vespertilionidae): roosting and foraging behaviour. *Canadian Journal of Zoology* 61:1487–1491.

Leonard, M.L., and M.B. Fenton. 1984. Echolocation calls of *Euderma maculatum* (Vespertilionidae): use in orientation and communication. *Journal of Mammalogy* 65:122–126.

Leslie, D.M., Jr., and B.S. Clark. 2002. Feeding habits of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*) relative to prey abundance. *Acta Chiropterologica* 4:173–182.

Lewis, S.E. 1995. Roost switching in bats: a review. *Journal of Mammalogy* 76:481–496.

Li, H., and K.T. Wilkins. 2014. Patch or mosaic: bat activity responds to fine-scale urban heterogeneity in a medium sized city in the United States. *Urban Ecosystems* 17:1013–1031.

Licht, P., and P. Leitner. 1967a, Behavioral responses to high temperatures in three species of California bats. *Journal of Mammalogy* 48:52–61.

Licht, P., and P. Leitner. 1967b. Physiological responses to high environmental temperatures in three species of microchiropteran bats. *Comparative Biochemistry and Physiology* 22:371–387.

Lindberg, M.S., W.L. Kendall, J.E. Hines, and M.G. Anderson. 2001. Combining band recovery data and Pollock's robust design to model temporary and permanent emigration. *Biometrics* 57:273–282.

Loeb, S.C. 2017. Adaptive response to land-use history and roost selection by Rafinesque's big-eared bats. *Journal of Mammalogy* 98:560–571.

Loeb, S.C., and E.R. Britzke. 2010. Intra- and interspecific responses to Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) social calls. *Acta Chiropterologica* 12:329–336.

Loeb, S.B., and Zarnoch, S.J. 2011. Seasonal and multiannual roost use by Rafinesque's big-eared bats in the Coastal Plain of South Carolina. Pages 111–120 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Loeb, S.C., M.J. Lacki, and D.A. Miller, eds. 2011a. *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina. 157 pp.

Loeb, S.C., M.J. Lacki, and D.A. Miller. 2011b. Conservation and management of eastern big-eared bats: an introduction. Pages 1–11 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Loeb, S.C., T.J. Rodhouse, L.E. Ellison, C.L. Lausen, J.D. Reichard, K.M. Irvine, T.E. Ingersoll, J.T.H. Coleman, W.E. Thogmartin, J.R. Sauer, C.M. Francis, M.L. Bayless, T.R. Stanley, and D.H. Johnson. 2015. A plan for the North American Bat Monitoring Program (NABat). U.S. Department of Agriculture Forest Service, General Technical Report SRS–208, Asheville, North Carolina. 100 pp.

Loucks, L.M.S., and W. Caire. 2007. Sex ratio variation of *Myotis velifer* (Chiroptera: Vespertilionidae) in Oklahoma. *Southwestern Naturalist* 52:67–74.

Louisiana Department of Wildlife and Fisheries. 2015. Draft 2015 Louisiana wildlife action plan. <*http://www.wlf.louisiana.gov/wildlife/wildlife-action-plan*>. Cited 5 September 2017.

Lowery, G.H., Jr. 1974. *The Mammals of Louisiana and its Adjacent Waters*. Louisiana State University Press, Baton Rouge, Louisiana. 565 pp.

Lu, S.–L., and Bleier, W.J. 1981. Renal morphology of *Macrotus* (Chiroptera, Phyllostomatidae). *Journal of Mammalogy* 62:181–182.

Lucas, J.S., S.C. Loeb, and P.G.R. Jodice. 2015. Roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in a pristine habitat at three spatial scales. *Acta Chiropterologica* 17:131–141.

Ludlow, M.E., and J.A. Gore. 2000. Effects of a cave gate on emergence patterns of colonial bats. *Wildlife Society Bulletin* 28:191–196.

Luszcz, T.M.J., and R.M.R. Barclay. 2016. Influence of forest composition and age on habitat use by bats in southwestern British Columbia. *Canadian Journal of Zoology* 94:145–153.

Lutch, D.J. 1996. *Maternity roost characteristics and habitat selection of three forest-dwelling bat species in Arizona*. M.S. Thesis. Arizona State University, Tempe, Arizona. 85 pp.

Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford, United Kingdom. 264 pp.

Maine Department of Inland Fisheries and Wildlife. 2016. State list of endangered and threatened species. <*www.maine.gov/ifw/wildlife/endangered/listed_species_me.htm*>. Cited 5 September 2017.

Maine, J.J., and J.G. Boyles. 2015. Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences* 112:12438–12443.

Mann, S.L., R.J. Steidl, and V.M. Dalton. 2002. Effects of cave tours on breeding *Myotis velifer*. *Journal of Wildlife Management* 66:618–624.

Manning, R.W. 1993. Systematics and evolutionary relationships of the long-eared myotis, *Myotis evotis* (Chiroptera: Vespertilionidae). *Special Publications of the Museum, Texas Tech University* 37:1–58.

Manning, R.W., and Jones, J.K., Jr. 1988. A new subspecies of fringed myotis, *Myotis thysanodes*, from the northwestern coast of the United States. *Occasional Papers, Museum of Texas Tech University* 123:1–6.

Manning, R.W., and Jones, J.K., Jr. 1989. *Myotis evotis*. *Mammalian Species* (329):1–5.

Manville, R.H. 1962. A plea for bat conservation. *Journal of Mammalogy* 43:571.

Marcot, B.G. 1984. Winter use of some northwestern California caves by western big-eared bats and long-eared Myotis. *Murrelet* 65:46.

Marquardt, S.R., and J.R. Choate. 2009. Influence of thermal environment on food habits of female cave myotis (*Myotis velifer*). *Southwestern Naturalist* 54:166–175.

Martin, C.O., A.S. McCartney, D. Richardson, A.W. Trousdale, and M.S. Wolters. 2011. Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in Mississippi: distribution, current status, and conservation needs. Pages 63–74 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Martin, D.B. 1992. Contaminant studies on endangered bats in northeastern Oklahoma. U.S. Fish and Wildlife Service, Ecological Services Field Office Report, Tulsa Oklahoma, 28 pp. <*https://catalog.data.gov/dataset/contaminant-studies-on-endangered-bats-in-northeastern-oklahoma*>. Cited 5 September 2017.

Martin, R.A., and B.G. Hawks. 1972. Hibernating bats of the Black Hills of South Dakota I: Distribution and habitat selection. *Bulletin of the New Jersey Academy of Science* 17:24–30.

Martin, R.L., J.T. Pawluk, and T.B. Clancy. 1966. Observations on hibernation of *Myotis subulatus*. *Journal of Mammalogy* 47:348–349.

Maryland Department of Natural Resources. 2005. Maryland wildlife diversity conservation plan. 679 pp. <*http://teaming.com/sites/default/files/Maryland%20Wildlife%20Action%20Plan.pdf*>. Cited 5 September 2017.

Maryland Department of Natural Resources. 2010. Rare, threatened, and endangered animals of Maryland. 26 pp. <*http://dnr.maryland.gov/wildlife/Pages/plants_wildlife/rte/rteanimals.aspx*>. Cited 5 September 2017.

Maryland Department of Natural Resources. 2016. Maryland state wildlife action plan. <*http://dnr.maryland.gov/wildlife/Pages/plants_wildlife/SWAP_home.aspx*>. Cited 5 September 2017.

Massachusetts Division of Fisheries and Wildlife. 2015. Massachusetts list of endangered, threatened and special concern species. <*http://www.mass.gov/eea/agencies/dfg/dfw/natural-heritage/species-information-and-conservation/mesa-list/list-of-rare-species-in-massachusetts.html*>. Cited 5 September 2017.

Mazurek, M.J. 2004. A maternity roost of Townsend's big-eared bats (*Corynorhinus townsendii*) in coast redwood basal hollows in northwestern California. *Northwestern Naturalist* 85:60–62.

Mazurek, M.J., and W.J. Zielinski. 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. *Forest Ecology and Management* 193:321–334.

McAllister, C.T., C.R. Bursey, and A.D. Burns. 2005. Gastrointestinal helminths of Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (Chiroptera: Vespertilionidae), from southwestern Arkansas, USA. *Comparative Parasitology* 72:121–123.

McAllister, C.T., C.R. Bursey, and R.C. Dowler. 2007. *Acanthatrium alicatai* (Trematoda: Lecithodendriidae) from two species of bats (Chiroptera: Vespertilionidae) in southwestern Texas. *Southwestern Naturalist* 52:597–600.

McCartney, A.S. 2007. Distribution and abundance of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) in Mississippi. U.S. Fish and Wildlife Service, Jackson, Mississippi, 65 pp. <*https://ecos.fws.gov/ServCat/Reference/Profile/40874*>. Accessed 13 September 2017.

McCartney, A. S., and W.M. McCartney. 2008. Bat surveys at Theodore Roosevelt National Wildlife Refuge Complex, 2007 with an emphasis on Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern Myotis (*Myotis austroriparius*). U.S. Fish and Wildlife Service, Jackson, Mississippi. 47 pp. https://ecos.fws.gov/ServCat/DownloadFile/52773?Reference=51929. Accessed 13 September 2017.

McDaniel, V.R., M.J. Harvey, R. Tumlison, and K.N. Paige. 1982. Status of the small-footed bat, *Myotis leibii leibii*, in the southern Ozarks. *Proceedings of the Arkansas Academy of Sciences* 36:92–94.

McDonnell, J.M. 2001. *Use of bridges as day roosts by bats in the North Carolina Coastal Plain*. North Carolina State University, M.S. Thesis. 74 pp.

McGregor, S.E., S.M. Alcorn, and G. Olin. 1962. Pollination and pollinating agents of the saguaro. *Ecology* 43:259–267.

Mead, J.I., and D.G. Mikesic. 2001. First fossil record of *Euderma maculatum* (Chiroptera: Vespertilionidae), eastern Grand Canyon, Arizona. *Southwestern Naturalist* 46:380–383.

Medeiros, J.L., and R.A. Heckmann. 1971. *Euderma maculatum* from California infected with rabies virus. *Journal of Mammalogy* 52:858.

Medlin, R.E., Jr., and T.S. Risch. 2008. Habitat associations of bottomland bats, with focus on Rafinesque's big-eared bat and southeastern myotis. *American Midland Naturalist* 160:400–412.

Menzel, J.M., M.A. Menzel, W.M. Ford, J.W. Edwards, S.R. Sheffield, J.C. Kilgo, and M.S. Bunch. 2003. The distribution of the bats of South Carolina. *Southeastern Naturalist* 2:121–152.

Menzel, J.M., M.A. Menzel, J.C. Kilgo, W.M. Ford, and J.W. Edwards. 2005. Bat response to Carolina bays and wetland restoration in the southeastern U.S. coastal plain. *Wetlands* 25:542–550.

Menzel, M.A., J.M. Menzel, W.M. Ford, J.W. Edwards, T.C. Carter, J.B. Churchill, and J.C. Kilgo. 2001. Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *American Midland Naturalist* 145:402–408.

Menzel, M.A, B.R. Chapman, W.M. Ford, J.M. Menzel, and J. Laerm. 2000. A review of the distribution and roosting ecology of bats in Georgia. *Georgia Journal of Science* 58:143–178.

Menzel, M.A., J.M. Menzel, W.M. Ford, J.W. Edwards, T.C. Carter, J.B. Churchill, and J.C. Kilgo. 2001. Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *American Midland Naturalist* 145:402–408.

Mering, E.D., and C.L. Chambers. 2012. Artificial roosts for tree-roosting bats in northern Arizona. *Wildlife Society Bulletin* 36:765–772.

Merriam, C.H. 1886. Description of a new species of bat from the western United States (*Vespertilio ciliolabrum* sp. nov.). *Proceedings of the Biological Society of Washington* 4:1–4.

Merritt, J.F. 1987. *Guide to the Mammals of Pennsylvania*. University of Pittsburgh Press, Pittsburgh, Pennsylvania. 408 pp.

Mickey, A.B. 1961. Record of the spotted bat from Wyoming. *Journal of Mammalogy* 42:401–402.

Miller, D.A. 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist* 2:59–72.

Miller, D.A., C.W. Stihler, D.B. Sasse, R. Reynolds, P. Van Deusen, and S.B. Castleberry. 2011. Conservation and management of eastern big-eared bats (*Corynorhinus* spp.). Pages 53–61 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Miller, G.S., Jr. 1897. Revision of the North American bats of the family Vespertilionidae. *North American Fauna* 13:1–135.

Miller, G.S., Jr. 1906. A bat new to the United States. *Proceedings of the Biological Society of Washington* 19:95–98.

Miller, G.S., Jr., and G.M. Allen. 1928. The American bats of the genera *Myotis* and *Pizonyx*. *Bulletin of the United States National Museum* 144:1–218.

Milligan, B.N. 1993. Carrying of young by female Yuma bats (*Myotis yumanensis*). *Northwestern Naturalist* 74:55–56.

Milligan, B.N., and R.M. Brigham. 1993. Sex ratio variation in the Yuma bat (*Myotis yumanensis*). *Canadian Journal of Zoology* 71:937–940.

Milner, J., C. Jones, and J.K. Jones, Jr. 1990. *Nyctinomops macrotis*: *Mammalian Species* (351):1–4.

Mirowsky, K.-M., P.A. Horner, R.W. Maxey, and S.A. Smith. 2004. Distributional records and roosts of southeastern myotis and Rafinesque's big-eared bat in eastern Texas. *Southwestern Naturalist* 49: 294–298.

Mississippi Department of Wildlife, Fisheries and Parks. 2005. Mississippi's comprehensive wildlife conservation strategy 2005–2015. 428 pp. <*http://climatechange.lta.org/wp-content/uploads/cct/2015/03/cwcs_MS.pdf*>. Cited 5 September 2017.

Mississippi Department of Wildlife, Fisheries and Parks. 2015. Mississippi's state wildlife action plan, 2015–2025. 704 pp. <*https://www.mdwfp.com/media/251788/mississippi_swap_revised_16_september_2016__reduced_.pdf*>. Cited 5 September 2017.

Missouri Department of Conservation. 2016. Missouri species and communities of conservation concern. 58 pp. <*https://archive.org/details/2016MOSpeciesOfConcern*>. Cited 5 September 2017.

Mohr, C.E. 1936. Notes on the least brown bat *Myotis subulatus leibii*. *Proceedings of the Pennsylvania Academy of Science* 10:62–65.

Mohr, C.E. 1942. Results of ten years' bat marking in Pennsylvania. *Proceedings of the Pennsylvania Academy of Science* 16:32–36.

Mohr, C.E. 1952. A survey of bat-banding in North America, 1932–1951. *American Caver* 14:3–13.

Mohr, C.E. 1972. The status of threatened species of cave-dwelling bats. *Bulletin of the National Speleological Society* 34:33–47.

Mollhagen, T.R., and M.A. Bogan. 1997. Bats of the Henry Mountains region of southeastern Utah. *Occasional Papers, Museum of Texas Tech University* 170:1–13.

Mollhagen, T.R., and M.A. Bogan. 2016. An inventory of bats in Arch Canyon, San Juan County, Utah. Pages 215–223 *in* R.W. Manning, J.R. Goetze, and F.D. Yancey, II, eds., *Contributions in Natural History: a Memorial Volume in Honor of Clyde Jones*. *Special Publications of the Museum, Texas Tech Uni-*

versity 65.

Mondul, A.M., J.W. Krebs, and J.E. Childs. 2003. Trends in national surveillance for rabies among bats in the United States (1993–2000). *Journal of the American Veterinary Medical Association* 222:633–639.

Montana Fish, Wildlife, and Parks. 2005. Montana's comprehensive fish and wildlife conservation strategy. 658 pp. <*http://fwp.mt.gov/fishAndWildlife/conservationInAction/fullplan.html*>. Cited 5 September 2017.

Montana Fish, Wildlife, and Parks. 2015a. Montana's species of concern. <*http://fwp.mt.gov/fishAndWildlife/species/speciesOfConcern/default.html*>. Cited 5 September 2017.

Montana Fish, Wildlife, and Parks. 2015b. Montana's state wildlife action plan. 441 pp. <*http://fwp.mt.gov/fishAndWildlife/conservationInAction/swap2015Plan.html*>. Cited 5 September 2017.

Moore, J.C. 1949. Putnam County and other Florida mammal notes. *Journal of Mammalogy* 30:57–66.

Moosman, P.R., Jr., H.W. Thomas, and J.P. Veilleux. 2007. Food habits of eastern small-footed bats (*Myotis leibii*) in New Hampshire. *American Midland Naturalist* 158:354–360.

Moosman, P.R., Jr., J.P. Veilleux, G.W. Pelton, and H.W. Thomas. 2013. Changes in capture rates in a community of bats in New Hampshire during the progression of white-nose syndrome. *Northeastern Naturalist* 20:552–558.

Moosman, P.R., Jr., D.P. Warner, R.H. Hendren, and M.J. Hosler. 2015. Potential for monitoring eastern small-footed bats on talus slopes. *Northeastern Naturalist* 22:NENHC–1–NENHC–13.

Morrell, T.E., and P. Craig. 1995. Temporal variation in fruit bats observed during daytime surveys in American Samoa. *Wildlife Society Bulletin* 23:36–40.

Morrell, T.E., M.J. Rabe, J.C. deVos, H. Green, and C.R. Miller. 1999. Bats captured in two ponderosa pine habitats in north-central Arizona. *Southwestern Naturalist* 44:501–506.

Morris, A.D., D.A. Miller, and M.C. Kalcounis–Rueppell. 2010. Use of forest edges by bats in a managed pine forest landscape. *Journal of Wildlife Management* 74:26–34.

Mumford, R.E. 1957. *Myotis occultus* and *Myotis yumanensis* breeding in New Mexico. *Journal of Mammalogy* 38:260.

Mumford, R.E., and J.O. Whitaker, Jr. 1982. *Mammals of Indiana*. Indiana University Press, Bloomington, Indiana. 537 pp.

Mumford, R.E., and D.A. Zimmerman. 1962. Notes on *Choeronycteris mexicana. Journal of Mammalogy* 43:101–102.

Mumford, R.E., L.L. Oakley, and D.A. Zimmerman. 1964. June bat records from Guadalupe Canyon, New Mexico. *Southwestern Naturalist* 9:43–45.

Munro, J.A., and I.M. Cowan. 1944. Preliminary report on the birds and mammals of Kootenay National Park, British Columbia. *Canadian Field-Naturalist* 58:34–51.

Nagorsen, D.W., and R.M. Brigham. 1993. *Bats of British Columbia*. Royal British Columbia Museum Handbook 1, The Mammals of British Columbia. University of British Columbia Press, Vancouver, British Columbia. 164 pp.

Nájera-Cortazar, L.A., S.T. Álvarez-Castañeda, and F. De Luna. 2015. An analysis of *Myotis peninsularis* (Vespertilionidae) blending morphometric and genetic datasets. *Acta Chiropterologica* 17:37–47.

Nature Serve. 2017. NatureServe explorer: natureserve online database. <*http://explorer.natureserve.org/*>. Cited 5 September 2017.

Navo, K.W. 2001. The survey and evaluation of abandoned mines for bat roosts in the West: guidelines for natural resource managers. *Proceedings of the Denver Museum of Nature and Science* 4:1–12.

Navo, K.W., and J.A. Gore. 2001. Distribution of the big free-tailed bat (*Nyctinomops macrotis*) in Colorado. *Southwestern Naturalist* 46:370–376.

Navo, K.W., J.A. Gore, and G.T. Skiba. 1992. Observations on the spotted bat, *Euderma maculatum*, in northwestern Colorado. *Journal of Mammalogy* 73:547–551.

Navo, K.W., L.R. Bonewell, A.J. Piaggio, N. Lamantia-Olson, and C.E. Wilkey. 2000. A Colorado case study to secure underground mines for bat habitat. Pages 153–157 *in* K.C. Vories and D. Throgmorton, eds., *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum, St. Louis, Missouri, November 14–16, 2000*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Navo, K.W., S.G. Henry, and T.E. Ingersoll. 2002. Observations of swarming by bats and band recoveries in Colorado. *Western North American Naturalist* 62:124–126.

Nebraska Game and Parks Commission. 2011. The Nebraska Natural Legacy Project state wildlife action plan (second edition): Appendices 8 and 9. 352 pp. <*http://outdoornebraska.gov/naturallegacyproject/*>. Cited 17 September 2017.

Nelson, S.L., M.A. Miller, E.J. Heske, and G.C. Fahey, Jr. 2000a. Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. *Ecography* 23:393–401.

Nelson, S.L., M.A. Miller, E.J. Heske, and G.C. Fahey, Jr. 2000b. Nutritional quality of leaves and unripe fruit consumed as famine foods by the flying foxes of Samoa. *Pacific Science* 54:301–311.

Neubaum, D.J. 2017. Bat composition and roosting habits of Colorado National Monument and McInnis Canyons National Conservation Area.: Colorado Parks and Wildlife Report, 104 pp. <*http://c10110.eos-intl.net/C10110/public/Index.aspx*>. Cited 5 November 2017.

Neubaum, D.J., and K.W. Navo. 2011. Acoustic sampling of bat species in Dinosaur National Monument. Colorado Division of Wildlife Report, 67 pp. <*http://c10110.eos-intl.net/ELIBSQL10_C10110_Documents/AcousticSamplingBats..DinosaurNM2011%20by%20NavoNeubaum.pdf*>. Cited 5 September 2017.

Neubaum, D.J., K.W. Navo, and J.L. Siemers. 2017. Guidelines for defining biologically important bat roosts: a case study from Colorado. *Journal of Fish and Wildlife Management* 8:272–282.

Neubaum, D.J., O'Shea, T.J., and K.R. Wilson. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats (*Eptesicus fuscus*) in Colorado. *Journal of Mammalogy* 87:470–479.

Nevada Department of Conservation and Natural Resources. 2015a. Nevada Natural Heritage Program. <*http://heritage.nv.gov/*>. Cited 5 September 2017.

Nevada Department of Conservation and Natural Resources. 2015b. Nevada Natural Heritage Program species lists. <*http://heritage.nv.gov/species/lists.php*>. Cited 5 September 2017.

Nevada Department of Wildlife. 2013. Nevada wildlife action plan. <*http://www.ndow.org/Nevada_Wildlife/Conservation/Nevada_Wildlife_Action_Plan/*>. Cited 5 September 2017.

New Hampshire Fish and Game Department. 2015. New Hampshire wildlife action plan, revised. <*http://www.wildlife.state.nh.us/wildlife/wap.html*>. Cited 5 September 2017.

New Jersey Department of Environmental Protection. 2008. New Jersey wildlife action plan for wildlife of greatest conservation need. 1,060 pp. <*http://www.nj.gov/dep/fgw/ensp/wap/pdf/wap_draft.pdf*> > Cited 5 September 2017.

New Mexico Department of Game and Fish. 2006. Comprehensive wildlife conservation strategy for New Mexico. 681 pp. <*http://teaming.com/sites/default/files/New%20Mexico%20Wildlife%20Action%20Plan.pdf*>. Cited 5 September 2017.

New Mexico Department of Game and Fish. 2012. Threatened and endangered species of New Mexico 2012 biennial review. 154 pp. <http://www.wildlife.state.nm.us/download/conservation/threatened-endangered-species/biennial-reviews/2012–Biennial-Review-Executive_Summary_and_Full_Text.pdf>. Cited 5 September 2017.

New Mexico Department of Game and Fish. 2015. Biota Information System of New Mexico. <*http://www.bison-m.org/*>. Cited 5 September 2017.

New York Department of Environmental Conservation. 2015a. List of endangered, threatened and special concern fish and wildlife species of New York State. <*http://www.dec.ny.gov/animals/7494.html*>. Cited 5 September 2017.

New York Department of Environmental Conservation. 2015b. New York State wildlife action plan final draft 2015. 107 pp. <*http://www.dec.ny.gov/animals/7179.html*> Cited 5 September 2017.

Nickel, P.A., and M.F. Hansen. 1967. Helminths of bats collected in Kansas, Nebraska and Oklahoma. *American Midland Naturalist* 78:481–486.

Nixon, A.E., J.C. Gruver, and R.M.R. Barclay. 2009. Spatial and temporal patterns of roost use by western long-eared bats (*Myotis evotis*). *American Midland Naturalist* 162:139–147.

Norberg, U.M., and Rayner, J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society, Series B Biological Sciences* 316:335–427.

Norberg, U.M.L., A.P. Brooke, and W.J. Trewhella. 2000. Soaring and non-soaring bats of the family Pteropodidae (flying foxes: *Pteropus* spp.): wing morphology and flight performance. *Journal of Experimental Biology* 203:651–664.

North Carolina Wildlife Resources Commission. 2014. Protected wildlife species of North Carolina. 8 pp. <*http://www.ncwildlife.org/Portals/0/Conserving/documents/protected_species.pdf*>. Cited 5 September 2017.

Ober, H.K., and J.P. Hayes. 2008. Prey selection by bats in forests of western Oregon. *Journal of Mammalogy* 89:1191–1200.

O'Farrell, M.J. 1970. Notes on the distribution of *Macrotus waterhousii* in southern Nevada. *Great Basin Naturalist* 30:53.

O'Farrell, M.J., and W.G. Bradley. 1970. Activity patterns of bats over a desert spring. *Journal of Mammalogy* 51:18–26.

O'Farrell, M.J., and E.H. Studier. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology* 54:18–30.

O'Farrell, M.J., and E.H. Studier. 1975. Population structure and emergence activity patterns in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) in northeastern New Mexico. *American Midland Naturalist* 93:368–376.

O'Farrell, M.J., and E.H. Studier. 1980. *Myotis thysanodes*. *Mammalian Species* (137):1–5.

Ohio Department of Natural Resources Division of Wildlife. 2015. Ohio's listed species: wildlife that are considered to be endangered, threatened, species of concern, special interest, extirpated, or extinct in Ohio. Ohio Department of Natural Resources Division of Wildlife Publication 5356 (R1015). 10 pp. <*https://wildlife.ohiodnr.gov/portals/wildlife/pdfs/publications/information/pub356.pdf*>. Cited 5 September 2017.

Ohlendorf, H.M. 1972. Observations on a colony of *Eumops perotis* (Molossidae). *Southwestern Naturalist* 17:297–300.

O'Keefe, J.M., and M. LaVoie. 2010. Maternity colony of eastern small-footed myotis (*Myotis leibii*) in a historic building. *Southeastern Naturalist* 10:381–383.

Oklahoma Department of Wildlife Conservation. 2005. Oklahoma comprehensive wildlife conservation strategy. 421 pp. <*https://www.wildlifedepartment.com/CWCS.htm*> Cited 5 September 2017.

Oklahoma Department of Wildlife Conservation. 2016. Oklahoma comprehensive wildlife conservation strategy: a strategic conservation plan for Oklahoma's rare and declining wildlife. 358 pp. <*https://www.wildlifedepartment.com/wildlifemgmt/cwcs.pdf* > Cited 5 September 2017.

Oklahoma Department of Wildlife Conservation. 2017. Eastern Oklahoma bat tests positive for white-nose syndrome. Oklahoma Department of Wildlife Conservation press release from April 17, 2017, <*https://www.wildlifedepartment.com/outdoor-news/eastern-oklahoma-bat-tests-positive-white-nose-syndrome*> Cited 5 September 2017.

Oliver, G.V. 2000. The bats of Utah: a literature review. Utah Division of Wildlife Resources, Publication Number 00–14, Salt Lake City, Utah. 140 pp. <*http://dwrcdc.nr.utah.gov/ucdc/viewreports/bats.pdf*> Cited 5 September 2017.

Olson, A.C., Jr. 1947. First record of *Choeronycteris mexicana* in California. *Journal of Mammalogy* 28:183–184.

Oregon Department of Fish and Wildlife. 2005. The Oregon conservation strategy. <*http://www.oregonconservationstrategy.org/*>. Cited 5 September 2017.

Oregon Department of Fish and Wildlife. 2008. Sensitive species. 11 pp. <http://www.dfw.state.or.us/wildlife/diversity/species/sensitive_species.asp > Cited 5 September 2017.

Ormsbee, P.C. 1996. Characteristics, use, and distribution of day roosts selected by female *Myotis volans* (long-legged myotis) in forested habitat of the central Oregon Cascades. Pages 124–130 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

Ormsbee, P.C., and W.C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. *Journal of Wildlife Management* 62:596–603.

Orr, R.T. 1956. The distribution of *Myotis thysanodes* in California. *Journal of Mammalogy* 37:545–546.

Osborne, C., P.M. Cryan, T.J. O'Shea, L.M., Oko, C. Ndaluka, C.H. Calisher, A.D. Berglund, L. Mead, M.L. Klavetter, R.A. Bowen, K.V. Holmes, and S.R. Dominguez. 2011. Alphacoronaviruses in New World bats: prevalence, persistence, phylogeny, and potential for interaction with humans. *PLoS ONE* 6:e19156. 11 pp.

O'Shea, T.J., and M.A. Bogan. eds. 2003. *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*: U.S. Geological Survey Information Technology Report ITR 2003–003, Reston, Virginia. 274 pp.

O'Shea, T.J., P.M. Cryan, E.A. Snider, E.W. Valdez, L.E. Ellison, and D.J. Neubaum. 2011a. Bats of Mesa Verde National Park, Colorado: composition, reproduction, and roosting habits. *Monographs of the Western North American Naturalist* 5:1–19.

O'Shea, T.J., P.M. Cryan, D.T.S. Hayman, R.K. Plowright, and D.G. Streicker. 2016a. Multiple mortality events in bats: a global review. *Mammal Review* 46:175–190.

O'Shea, T.J., L.E. Ellison, D.J. Neubaum, M.A. Neubaum, C.A. Reynolds, and R.A. Bowen. 2010. Recruitment in a Colorado population of big brown bats: breeding probabilities, litter size, and first-year survival. *Journal of Mammalogy* 91:418–428.

O'Shea, T.J., L.E. Ellison, and T.R. Stanley. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. Pages 297–336 *in* W.L. Thompson, ed., *Sampling Rare or Elusive Species*. Island Press, Washington, D.C.,

O'Shea, T.J., L.E. Ellison, and T.R. Stanley. 2011c. Adult survival and population growth rate in Colorado big brown bats. *Journal of Mammalogy* 92:433–443.

O'Shea, T.J., C. Klinger, L.A. Smythe, L. Wilkinson, and J.P. Dumbacher. 2016b. Survey of the bat fauna, Desert National Wildlife Refuge, Nevada. *Western North American Naturalist* 76:501–508.

O'Shea, T.J., D.J. Neubaum, M.A. Neubaum, P.M. Cryan, L.E. Ellison, T.R. Stanley, C.E. Rupprecht, W.J. Pape, and R.A. Bowen. 2011b. Bat ecology and public health surveillance for rabies in an urbanizing region of Colorado. *Urban Ecosystems* 14:665–697.

O'Shea, T.J., and T.A. Vaughan. 1999. Population changes in bats from central Arizona: 1972 and 1997. *Southwestern Naturalist* 44:495–500.

Oyler-McCance, S.J., E.W. Valdez, T.J. O'Shea, and J.A. Fike. 2013. Genetic characterization of the Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*) using mitochondrial DNA sequence data. *Journal of Mammalogy* 94:1030–1036.

Painter, M.L., C.L. Chambers, M. Siders, R.R. Doucett, J.O. Whitaker, Jr., and D.L. Phillips. 2009. Diet of spotted bats (*Euderma maculatum*) in Arizona as indicated by fecal analysis and stable isotopes. *Canadian Journal of Zoology* 87:865–875.

Pape, W.J., T.D. Fitzsimmons, and R.E. Hoffman. 1999. Risk for rabies transmission from encounters with bats, Colorado, 1977–1996. *Emerging Infectious Diseases* 5:433–437.

Paradiso, J.L., and A.M. Greenhall. 1967. Longevity records for American bats. *American Midland Naturalist* 78:251–252.

Parish, D.A., and C. Jones. 1999. Big free-tailed bat, *Nyctinomops macrotis.* Pages 130–131 *in* Wilson, D.E., and Ruff, S., eds., *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, Washington, D.C.

Parker, D.I., B.E. Lawhead, and J.A. Cook. 1997. Distributional limits of bats in Alaska. *Arctic* 50:256–265.

Parker, H.C. 1952. Two new records of the spotted bat in California. *Journal of Mammalogy* 33:480–482.

Parkinson, A. 1979. Morphological variation and hybridization in *Myotis yumanensis sociabilis* and *M. lucifugus carissima*. *Journal of Mammalogy* 60:489–504.

Parlos, J.A. 2008. *Population genetic structure of a cave-dwelling bat*, *Myotis velifer.* M.S. Thesis. Texas State University-San Marcos, Texas. 81 pp.

Patriquin, K.J., M.J. Leonard, H.G. Broders, and C.J. Garroway. 2010. Do social networks of female northern long-eared bats vary with reproductive period and age? *Behavioral Ecology and Sociobiology* 64:899–913.

Pearson, E.W. 1962. Bats hibernating in silica mines in southern Illinois. *Journal of Mammalogy* 43:27–33.

Pearson, O.P., M.R. Koford, and A.K. Pearson. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquii*) in California. *Journal of Mammalogy* 33:273–320.

Pennsylvania Game Commission. 2015. Pennsylvania wildlife action plan 2015–2025. <*http://www.pgc.pa.gov/WILDLIFE/WILDLIFEACTIONPLAN/Pages/default.aspx*> Cited 5 September 2017.

Perkins, J.M., J.M. Barss, and J. Peterson. 1990. Winter records of bats in Oregon and Washington. *Northwestern Naturalist* 71:59–62.

Perlmeter, S.I. 1996. Bats and bridges: patterns of night roost activity in the Willamette National Forest. Pages132–150 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

Perry, T.W., P.M. Cryan, S.R. Davenport, and M.A. Bogan. 1997. New locality for *Euderma maculatum* (Chiroptera: Vespertilionidae) in New Mexico. *Southwestern Naturalist* 42:99–101.

Petryszyn, Y., and E.L. Cockrum. 1990. *Mammals of the Quitobaquito Management Area, Organ Pipe Cactus National Monument, Arizona*. Cooperative National Park Resources Studies Unit, School of Renewable Natural Resources, University of Arizona, Tucson, Technical Report 36. 32 pp.

Piaggio, A.J., and S.L. Perkins. 2005. Molecular phylogeny of North American long-eared bats (Vespertilionidae: *Corynorhinus*): inter- and intraspecific relationships inferred from mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* 37:762–775.

Piaggio, A.J., K.W. Navo, and C.W. Stihler. 2009. Intraspecific comparison of population structure, genetic diversity, and dispersal among three subspecies of Townsend's big-eared bats, *Corynorhinus townsendii townsendii*, *C. t. pallescens*, and the endangered *C. t. virginianus*. *Conservation Genetics* 10:143–159.

Piaggio, A.J., D.A. Saugey, and D.B. Sasse. 2011. Phylogenetic and population genetic assessment of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). Pages 85–99 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Piaggio, A.J., E.W. Valdez, M.A. Bogan, and G.S. Spicer. 2002. Systematics of *Myotis occultus* (Chiroptera: Vespertilionidae) inferred from sequences of two mitochondrial genes. *Journal of Mammalogy* 83:386–395.

Pierson, E.D. 1989. Help for Townsend's big-eared bat in California. *Bats* 7:5–8.

Pierson, E.D., and G.M. Fellers. 1998. Distribution and ecology of the big-eared bat, *Corynorhinus* (=*Plecotus*) *townsendii* in California. U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division, Species at Risk Program, Washington, D.C. 93 pp. <*https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=24003*>. Cited 5 September 2017.

Pierson, E.D., and W.E. Rainey. 1992. The biology of flying foxes of the genus *Pteropus*: a review. Pages 1–17 *in* D.E. Wilson and G.L. Graham, eds., *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference.* U.S. Fish and Wildlife Service, Biological Report 90.

Pierson, E.D., and W.E. Rainey. 1998a. Distribution, status, and management of Townsend's big-eared bat (*Corynorhinus townsendii*) in California. California Department of Fish and Game, Bird and Mammal Conservation Program, Final Report, Contract FG7129, BMCP Technical Report 96–7 (Updated May 1998). Sacramento, California. 34 pp.

Pierson, E.D., and W.E. Rainey. 1998b. Distribution of the spotted bat, *Euderma maculatum*, in California. *Journal of Mammalogy* 79:1296–1305.

Pierson, E.D., and W.E. Rainey. 1998c. Distribution, habitat associations, status, and survey methodologies for three molossid bat species (*Eumops perotis*, *Nyctinomops femorosaccus*, *Nyctinomops macrotis*) and the vespertilionid (*Euderma maculatum*). California Department of Fish and Game, Bird and Mammal Conservation Program, Final Report, Contract FG2328WM, Sacramento, California. 61 pp.

Pierson, E.D., and W.E. Rainey. 1998d. Arizona myotis, *Myotis occultus*, Pages 52–53 *in* B.C. Bolster, ed., *Terrestrial Mammal Species of Special Concern in California*. California Department of Fish and Game Wildlife Management Division, Nongame Bird and Mammal Conservation Program, Draft Report, Contract FG3146WM. Sacramento, California. <*https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=84481*>. Cited 5 September 2017.

Pierson, E.D., W.E. Rainey, and L.S. Chow. 2006. Bat use of the giant sequoia groves in Yosemite National Park. Report prepared for the Yosemite Fund and Yosemite National Park, Yosemite, California. 146 pp. <*https://www.nps.gov/yose/learn/nature/upload/Bat%20study%20Pierson%202006.pdf*> Cited 5 September 2017.

Pierson, E.D., W.E. Rainey, and C.J. Corben. 2001. Seasonal patterns of bat distribution along an altitudinal gradient in the Sierra Nevada. Report to the California Department of Transportation, California State University at Sacramento Foundation, Yosemite Association, and Yosemite Fund, Yosemite California. 70 pp. <*https://www.nps.gov/yose/learn/nature/upload/Bat.study.Pierson.2001.pdf*> Cited 5 September 2017.

Pierson, E.D., W.E. Rainey, and D.M. Koontz. 1991. Bats and mines: experimental mitigation for Townsend's big-eared bat at the McLaughlin Mine in California. Pages 31–42 *in* R.D. Comer, ed., *Issues and Technology in the Management of Impacted Wildlife: Proceedings of a Conference, April 8–10, 1991.* Thorne Ecological Institute, Snowmass, Colorado.

Pierson, E.D., W.E. Rainey, P. Cox, and T. Elmqvist. 1992. *Pteropus samoensis* Samoa fruit bat. Pages 127–129 *in* S.P. Mickleburgh, A.M. Hutson, and P.A. Racey, eds., *Old World Fruit Bats: An Action Plan for their Conservation.* International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Pierson, E.D., T. Elmqvist, W.E. Rainey, and P.A. Cox. 1996a. Effects of tropical cyclonic storms on flying fox populations on the South Pacific islands of Samoa. *Conservation Biology* 10:438–451.

Pierson, E.D., W.E. Rainey, and R.M. Miller. 1996b. Night roost sampling: a window on the forest bat community in northern California. Pages 151–163 *in* R.M.R. Barclay and R.M. Brigham, eds., *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia.* Research Branch, British Columbia Ministry of Forestry, Working Paper 23/1996. Victoria, British Columbia.

Pierson, E.D., M.C. Wackenhut, J.S. Altenbach, P. Bradley, P. Call, D.L. Genter, C.E. Harris, B.L. Keller, B. Lengus, L. Lewis, B. Luce, K.W. Navo, J.M. Perkins, S. Smith, and L. Welch. 1999. Species conservation assessment and strategy for Townsend's big-eared bat (*Corynorhinus townsendii townsendii* and *Corynorhinus townsendii pallescens*). Department of Fish and Game, Idaho Conservation Effort, Boise, Idaho. 42 pp.

Piorkowski, M.D., and T.J. O'Connell. 2010. Spatial pattern of summer bat mortality from collisions with wind turbines in mixed-grass prairie. *American Midland Naturalist* 164:260–269.

Pitts, R.M., and J.J. Scharninghausen. 1986. Use of cliff swallow and barn swallow nests by the cave bat, *Myotis velifer*, and the free-tailed bat, *Tadarida brasiliensis*. *Texas Journal of Science* 38:265–266.

Pitts, R.M., G.T. Schimmelpfenig, and J.R. Choate. 1996. The big free-tailed bat, *Nyctinomops macrotis*, in Missouri. *Southwestern Naturalist* 41:86–87.

Platenberg, R.J., F.E. Hayes, D.B. McNair, and J.J. Pierce. 2005. *A Comprehensive Wildlife Conservation Plan for the U.S. Virgin Islands.* Division of Fish and Wildlife, St. Thomas, U.S. Virgin Islands. 216 pp.

Poché, R.M. 1975. New Record of *Euderma maculatum* from Arizona. *Journal of Mammalogy* 56:931–933.

Poché, R.M. 1979. Notes on the big free-tailed bat (*Tadarida macrotis*) from southwest Utah, U.S.A. *Mammalia* 43:125–126.

Poché, R.M. 1981. Ecology of the spotted bat (*Euderma maculatum*) in southwest Utah. Utah Department of Natural Resources, Division of Wildlife Resources, Publication 81–1, Salt Lake City, Utah. 63 pp.

Poché, R.M., and G.L. Bailie. 1974. Notes on the spotted bat (*Euderma maculatum*) from southwest Utah. *Great Basin Naturalist* 34:254–256.

Poché, R.M., and G.A. Ruffner. 1975. Roosting behavior of male *Euderma maculatum* from Utah. *Great Basin Naturalist* 35:121–122.

Ports, M.A., and P.V. Bradley. 1996. Habitat affinities of bats from northeastern Nevada. *Great Basin Naturalist* 56:48–53.

Powers, K.E., R.J. Reynolds, W. Orndorff, and W.M. Ford. 2015. Post-white-nose syndrome trends in Virginia's cave bats, 2008–2013. *Journal of Ecology and Natural Environment* 6:56–64.

Prendergast, J.A., W.E. Jensen, and S.D. Roth. 2010. Trends in abundance of hibernating bats in a karst region of the southern Great Plains. *Southwestern Naturalist* 55:331–339.

Priday, J., and B. Luce. 1999. New distributional records for spotted bat (*Euderma maculatum*) in Wyoming. *Great Basin Naturalist* 59:97–101.

Psyllakis, J.M., and R.M. Brigham., 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management* 223:93–102.

Puerto Rico Department of Natural and Environmental Resources. 2015. Puerto Rico state wildlife action plan: ten-year review. San Juan, Puerto Rico. 187 pp. <*http://drna.pr.gov/historico/PRSWAP2015.pdf*> Cited 5 September 2017.

Quay, W.B. 1948. Notes on some bats from Nebraska and Wyoming. *Journal of Mammalogy* 29:181–182.

Rabe, M.J., and R.S. Rosenstock. 2005. Influence of water size and type on bat captures in the lower Sonoran desert. *Western North American Naturalist* 65:87–90.

Rabe, M.J., T.E. Morrell, H. Green, J.C. deVos, Jr., and C.R. Miller. 1998a. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management* 62: 612–621.

Rabe, M.J., M.S. Siders, C.R. Miller, and T.K. Snow. 1998b. Long foraging distance for a spotted bat (*Euderma maculatum*) in northern Arizona. *Southwestern Naturalist* 43:266–269.

Racey, P.A., and A.C. Entwistle. 2000. Life-history and reproductive strategies of bats. Pages 363–414 *in* E.G. Crichton and P.H. Krutzsch, eds., *Reproductive Biology of Bats*. Academic Press, San Diego, California.

Rancourt, S.J., M.I. Rule, and M.A. O'Connell. 2005. Maternity roost site selection of long-eared myotis, *Myotis evotis*. *Journal of Mammalogy* 86:77–84.

Raun, G.G. 1960. A mass die-off of the Mexican brown bat, *Myotis velifer*, in Texas. *Southwestern Naturalist* 5:104–105.

Raun, G.G., and J.K. Baker. 1958. Some observations of Texas cave bats. *Southwestern Naturalist* 3: 102–106.

Rausch, R.L. 1975. Cestodes of the genus *Hymenolepis* Weinland, 1858 (*sensu lato*) from bats in North America and Hawaii. *Canadian Journal of Zoology* 53:1537–1551.

Reduker, D.W., T.L. Yates, and I.F. Greenbaum. 1983. Evolutionary affinities among southwestern long-eared *Myotis* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 64:666–677.

Reeder, W.G., and R.B. Cowles. 1951. Aspects of thermoregulation in bats. *Journal of Mammalogy* 32: 389–403.

Reisen, W.K., M.L. Kennedy, and N.T. Reisen. 1976. Winter ecology of ectoparasites collected from hibernating *Myotis velifer* (Allen) in southwestern Oklahoma (Chiroptera: Vespertilionidae). *Journal of Parasitology* 62:628–635.

Reynolds, R.P. 1981. Elevational record for *Euderma maculatum* (Chiroptera: Vespertilionidae). *Southwestern Naturalist* 26:91–92.

Rhode Island Division of Fish and Wildlife. 2015. Rhode Island wildlife action plan. 17 pp. <*http://www.dem.ri.gov/programs/bnatres/fishwild/swap/sgcnsci.pdf*> Cited 5 September 2017.

Rice, C.L. 2009. *Roosting ecology of Corynorhinus rafinesquii* (*Rafinesque's big-eared bat*) *and Myotis austroriparius* (*southeastern myotis*) *in tree cavities found in a northeastern Louisiana bottomland hardwood forest streambed*. M.S. Thesis. University of Louisiana at Monroe, Monroe, Louisiana. 124 pp.

Rice, D.W. 1957. Life history and ecology of *Myotis austroriparius* in Florida. *Journal of Mammalogy* 38: 15–32.

Richardson, D. 2007. Helping nature provide hollow trees for bats. *Bats* 24:6–8.

Richardson, J.H., R.L. Ramsey, and L.E. Starr. 1966. Bat rabies in Georgia, 1956–65. *Public Health Reports* 81:1031–1035.

Riedle, T.D.H., and R.S. Matlack. 2013. Bats of Palo Duro Canyon State Park, Texas: community composition, abundance, and seasonal activity. *Western North American Naturalist* 73:89–97.

Ritzi, C.M. 1999. Utilization of cliff swallow (*Petrochelidon pykrrhonata*) nests in West Texas by cave myotis (*Myotis velifer*). *Southwestern Naturalist* 44:414–415.

Ritzi, C.M., L.K. Ammerman, M.T. Dixon, and J.V. Richerson. 2001. Bat ectoparasites from the Trans-Pecos region of Texas, including notes from Big Bend National Park. *Journal of Medical Entomology* 38:

400–404.

Ritzi, C.M., C.W. Walker, and R.L. Honeycutt. 1998. *Myotis velifer* use of cave swallow nests. *Texas Journal of Science* 50:175–176.

Roble, S.M. 2004. Notes on an autumn roost of an eastern small-footed bat (*Myotis leibii*). *Banisteria* 23: 42–44.

Roby, P.L., M.W. Gumbert, P.L. Sewell, and S.W. Brewer. 2011. Characteristics of roosts used by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) on Camp Mackall, North Carolina. Pages 101–110 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Rodeck, H.G. 1961. Another spotted bat from New Mexico. *Journal of Mammalogy* 42:401.

Rodhouse, T.J., and K.J. Hyde. 2014. Roost and forage site fidelity of western small-footed myotis (*Myotis ciliolabrum*) in an Oregon desert canyon. *Western North American Naturalist* 74:241–248.

Rodhouse, T.J., M.F. McCaffrey, and R.G. Wright. 2005. Distribution, foraging behavior, and capture results of the spotted bat (*Euderma maculatum*) in central Oregon. *Western North American Naturalist* 65:215–222.

Rodhouse, T.J., P.C. Ormsbee, K.M. Irvine, L.A. Vierling, J.M. Szewczak, and K.T. Vierling. 2015. Establishing conservation baselines with dynamic distribution models for bat populations facing imminent decline. *Diversity and Distributions* 21:1401–1413.

Rodhouse, T.J., S.A. Scott, P.C. Ormsbee, and J.M. Zinck. 2008. Field identification of *Myotis yumanensis* and *Myotis lucifugus*: a morphological evaluation. *Western North American Naturalist* 68:437–443.

Rodhouse, T.J., S.A. Scott, P.C. Ormsbee, and J.M. Zinck. 2009. On differentiating *Myotis yumanensis* and *Myotis lucifugus* in the field: a reply to Carraway. *Western North American Naturalist* 69:279–280.

Rodriguez, R.M., and L.K. Ammerman. 2004. Mitochondrial DNA divergence does not reflect morphological difference between *Myotis californicus* and *Myotis ciliolabrum*. *Journal of Mammalogy* 85:842–851.

Rodríguez-Durán, A. 1998. Nonrandom aggregations and distribution of cave-dwelling bats in Puerto Rico. *Journal of Mammalogy* 79:141–146.

Rodríguez-Durán, A., and W. Feliciano-Robles. 2015. Impact of wind facilities on bats in the Neotropics. *Acta Chiropterologica* 17:365–370.

Roehrs, Z.P., B.S. Coyner, K.N. King, D.L. Martinez, J.K. Braun, M.J. Hamilton, D.M. Leslie, Jr., and R.A. Van Den Bussche. 2008. New records of mammals from western Oklahoma. *Occasional Papers of the Museum, Texas Tech University* 273:1–15.

Rohweder, M.R. 2015. Kansas wildlife action plan. Ecological Services Section, Kansas Department of Wildlife, Parks and Tourism in cooperation with the Kansas Biological Survey Report. 176 pp. <*http://ksoutdoors.com/content/download/47332/483537/file/Complete%20Plan.pdf*> Cited 5 September 2017.

Ross, A. 1961. Notes on food habits of bats. *Journal of Mammalogy* 42:66–71.

Ross, A. 1964. *Ecological aspects of the food habits of some insectivorous bats*. Ph.D. Dissertation, University of Arizona. 99 pp.

Ross, A. 1967. Ecological aspects of the food habits of insectivorous bats. *Proceedings of the Western Foundation of Vertebrate Zoology* 1:205–264.

Rowlett, R.A. 1972. First records of *Eumops perotis* and *Microtus ochrogaster* in New Mexico. *Journal of Mammalogy* 53:640.

Ruffner, G.A., N.J. Czaplewski, and S.W. Carothers. 1978. Distribution and natural history of some mammals from the Inner Gorge of the Grand Canyon, Arizona. *Journal of the Arizona-Nevada Academy of Science* 13:85–91.

Ruffner, G.A., R.M. Poché, M. Meierkord, and J.A. Neil. 1979. Winter bat activity over a desert wash in southwestern Utah. *Southwestern Naturalist* 24:447–453.

Russell, A.L., V.A. Brown, R.C.B. Utzurrum, A.P. Brooke, L.A. Wolf, and G.F. McCracken. 2016. Comparative phylogeography of *Pteropus samoensis* and *P. tonganus* (Pteropodidae: Chiroptera) in the South Pacific. *Acta Chiropterologica* 18:325–335.

Ryan, J.M., D.A. Stilwell, and N.J. Morse. 1992. An evaluation of contaminant exposure of three endangered bat species in Virginia. U.S. Fish and Wildlife Service, Environmental Contaminants Branch, Virginia Field Office Report. 26 pp. <*https://ecos.fws.gov/ServCat/DownloadFile/21467?Reference=22948*> Cited 5 September 2017.

Sample, B.E., and R.C. Whitmore. 1993. Food habits of the endangered Virginia big-eared bat in West Virginia. *Journal of Mammalogy* 74:428–435.

Sanches, E.M.C., L. Ferreiro, C.P., Andrade, S.M., Pacheco, J.M. Santurio, L. Almeida, A. Spanamberg, and G. Wissmann. 2012. Real-time PCR and nested-PCR assays for detection of *Pneumocystis* sp. in lung tissues of bats. *Acta Scientiae Veterinariae* 40:1070.

Sasse, D.B. 1995. *Summer roosting ecology of cavity-dwelling bats in the White Mountain National Forest.* M.S. Thesis. University of New Hampshire. 65 pp.

Sasse, D.B., and D.A. Saugey. 2008. Rabies prevalence among and new distribution records of Arkansas bats. *Journal of the Arkansas Academy of Science* 62:159–160.

Sasse, D.B., and D.A. Saugey. 2014. Protection of water wells used as winter roosts by Rafinesque's big-eared bats. *Bat Research News* 55, p.17–20.

Sasse, D.B., D.A. Saugey, and D.R. England. 2011. Winter roosting behavior of Rafinesque's big-eared bat in southwestern Arkansas. Pages 123–128 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Sasse, D.B., T.S. Risch, D.A. Saugey, M.J. Harvey, J.D. Wilhide, R.K. Redman, J.J. Jackson, T. Klotz, and P.R. Moore. 2013. New records of the eastern small-footed bat (*Myotis leibii*) in Arkansas. *Journal of the Arkansas Academy of Science* 67:214–216.

Sastre, N., O. Francino, J.N. Curti, T.C. Armenta, D.L. Fraser, R.M. Kelly, E. Hunt, K. Silbermayr, C. Zewe, A. Sańchez, and L. Ferrer. 2016. Detection, prevalence and phylogenetic relationships of *Demodex* spp and further skin prostigmata mites (Acari, Arachnida) in wild and domestic mammals. *PLoS ONE* 11:e0165765. 20 pp.

Saugey, D.A., G.A. Heidt, and D.R. Heath. 1988. Utilization of abandoned mine drifts and fracture caves by bats and salamanders: unique subterranean habitat in the Ouachita Mountains. Pages 64–71 *in* R.C. Szaro, K.S. Severson, and D.R. Patton, eds., *Management of Amphibians, Reptiles, and Small Mammals in North America: Proceedings of the Symposium.* U.S. Department of Agriculture Forest Service, General Technical Report RM–166, Fort Collins, Colorado.

Saugey, D.A., D.R. Heath, and G.A. Heidt. 1989. The bats of the Ouachita Mountains. *Arkansas Academy of Science Proceedings* 43:71–77.

Saugey, D.A., V.R. McDaniel, D.R. England, M.C. Rowe, L.R. Chandler-Mozisek, and B.G. Cochran. 1993. Arkansas range extensions of the eastern small-footed bat (*Myotis leibii*) and northern long-eared bat (*Myotis septentrionalis*), and additional county records for the silver-haired bat (*Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), and Rafinesque's big-eared bat (*Plecotus rafinesquii*). *Proceedings of the Arkansas Academy of Science* 47:102–106.

Saunders, E.H. 2015. *Bat assemblage and selection of maternity roosts in a post-wildfire landscape.* M.S. Thesis. Northern Arizona University, Flagstaff, Arizona. 117 pp.

Saunders, M.B., and R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology* 73:1335–1345.

Scanlon, A.T., S. Petit, M. Tuiwawa, and A. Naikatini. 2014. High similarity between a bat-serviced plant assemblage and that used by humans. *Biological Conservation* 174:111–119.

Scheffer, T.H. 1930. Bat matters. *Murrelet* 11:11–13.

Schmidly, D.J. 1991. *The Bats of Texas.* Texas A&M University Press, College Station, Texas.188 pp.

Schmidt, C.A. 2014. *Bat habitat and radon concentrations at roosts in abandoned uranium mines*. M.S. Thesis. Northern Arizona University. 78 pp.

Schmidt, S.L. 1999. *Activity patterns of California leaf-nosed and other bats at wildlife water developments in the Sonoran Desert*. M.S. Thesis. University of Arizona, Tuscon, Arizona. 119 pp.

Schneider, N.J., J.E. Scatterday, A.L. Lewis, W.L. Jennings, H.D. Venters, and A.V. Hardy. 1957. Rabies in bats in Florida. *American Journal of Public Health* 47:983–989.

Schowalter, D.B. 1980. Swarming, reproduction, and early hibernation of *Myotis lucifugus* and *M. volans* in

Alberta, Canada. *Journal of Mammalogy* 61:350–354.

Scott, P.E. 2004. Timing of *Agave palmeri* flowering and nectar-feeding bat visitation in the Peloncillos and Chiricahua mountains. *Southwestern Naturalist* 49:425–434.

Scott, S.A. 2005. *Identification and distribution of Myotis yumanensis and Myotis lucifugus bats in Oregon*. M.S. Thesis. Portland State University, Portland, Oregon. 204 pp.

Sealander, J.A., and G.A. Heidt. 1990. *Arkansas Mammals: Their Natural History, Classification, and Distribution*. University of Arkansas Press, Fayetteville, Arkansas. 308 pp.

Senger, C.M., R. Senger, D., Senger, and S. Senger. 1974. Winter records of myotid bats in western Washington. *Murrelet* 55:13–14.

Seville, R.S., and J. Gruver. 2004. Species of *Eimeria* (Apicomplexa: Eimeriidae) from bats (Chiroptera: Vespertilionidae) in central Wyoming. *Journal of Parasitology* 90:348–351.

Shabman, R.S., S. Shrivastava, T. Tsibane, O. Attie, A. Jayaprakash, C.E. Mire, K.E. Dilley, V. Puri, T.B. Stockwell, T.W. Geisbert, R.Sachidanandam, and C.F. Basler. 2016. Isolation and characterization of a novel gammaherpesvirus from a microbat cell line. *Msphere* 1:e00070–15. 15 pp.

Shankar, V., L.A. Orciari, C. De Mattos, I.V. Kuzmin, W.J. Pape, T.J. O'Shea, and C.E. Rupprecht. 2005. Genetic divergence of rabies viruses from bat species of Colorado, USA. *Vector-Borne and Zoonotic Diseases* 5:330–341.

Sherman, H.B. 1930. Birth of the young of *Myotis austroriparius*. *Journal of Mammalogy* 11:495–503.

Sherwin, R.E., and W.L. Gannon. 2005. Documentation of an urban winter roost of the spotted bat (*Euderma maculatum*). *Southwestern Naturalist* 50:402–407.

Sherwin, R.E., D. Stricklan, and D.S. Rogers. 2000. Roosting affinities of Townsend's big-eared bat (*Corynorhinus townsendii*) in northern Utah. *Journal of Mammalogy* 81:939–947.

Sherwin, R.E., J.S. Altenbach, and S. Haymond. 2002. The responses of bats to gates. Pages 333–338 *in* K.C. Vories and D. Throgmorton, eds., *Bat Gate Design: A Technical Interactive Forum, Austin, Texas, March 4–6, 2002*. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois.

Sherwin, R.E., J.S. Altenbach, and D.L. Waldien. 2009. Managing abandoned mines for bats. Bat Conservation International, Austin, Texas. 6 pp. <*https://www.batcon.org/pdfs/batsmines/nrcs_brochure.pdf*> Cited 5 September 2017.

Sherwin, R.E., W.L. Gannon, and J.S. Altenbach. 2003. Managing complex systems simply: understanding inherent variation in the use of roosts by Townsend's big-eared bat. *Wildlife Society Bulletin* 31:62–72.

Siders, M.S., and W. Jolley. 2009. Roost sites of Allen's lappet-browed bats (*Idionycteris phyllotis*). *Southwestern Naturalist* 54:201–203.

Siders, M.S., M.J. Rabe, T.K. Snow, and K. Yasuda. 1999. Long foraging distances in two uncommon bat species (*Euderma maculatum* and *Eumops perotis*) in northern Arizona. Pages 113–122 *in* C. van Riper, III and M.A. Stuart, eds., *Proceedings of the 4th Biennial Conference of Research on the Colorado Plateau, Flagstaff, Arizona, 6–10 November 1997.* United States Geological Survey/FRESC Rep. Ser. USGSFRESC/COPL/1999/16, Corvallis, Oregon.

Sidner, R., and R. Davis. 1994. Bat inventory of riparian areas of Fort Huachuca Military Reservation. Arizona Game and Fish Heritage Fund Report I92019, Phoenix, Arizona. 29 pp.<*http://azmemory.azlibrary.gov/cdm/ref/collection/statepubs/id/16792*> Cited 5 September 2017.

Siemers, J. 2002. A survey of Colorado's caves for bats. Colorado Heritage Program Report, Fort Collins, Colorado. 20 pp. <*http://www.cnhp.colostate.edu/download/documents/2002/Cave_Inventory_report.pdf*> Cited 5 September 2017.

Siemers, J., and D.J. Neubaum. 2015. White River National Forest cave bat survey and monitoring—2015. Colorado Natural Heritage Program Report, Fort Collins, Colorado. 40 pp. <*http://c10110.eos-intl.net/elibsql10_C10110_Documents/WhiteRiverNFBatSurveyMonitor2015.pdf*>. Cited 5 September 2017.

Simmons, J.A., and M.J. O'Farrell. 1977. Echolocation by the long-eared bat, *Plecotus phyllotis. Journal of Comparative Physiology A* 122:201–214.

Simmons, N.B. 2005. Chiroptera. Pages 312–529 *in* D.E. Wilson, and D.M. Reeder, eds., *Mammal Species of the World: a Taxonomic and Geographic Reference* (3rd ed.). Johns Hopkins University Press, Baltimore, Maryland. <*https://www.departments.bucknell.edu/biology/resources/msw3/*> Cited 5 September 2017.

Sinavaiana, C., and J. Enright. 1992. The cultural significance of the flying fox in Samoa: a legendary view. Pages 36–38 *in* D.E. Wilson and G.L. Graham, eds., *Pacific Flying Foxes: Proceedings of an International Conservation Conference.* U.S. Fish and Wildlife Service, Biological Report 90.

Smith, S.J., D.M. Leslie, Jr., M.J. Hamilton, J.B. Lack, and R.A. Van Den Bussche. 2008. Subspecific affinities and conservation genetics of western big-eared bats (*Corynorhinus townsendii pallescens*) at the edge of their distributional range. *Journal of Mammalogy* 89:799–814.

Snider, E.A. 2009. *Post-fire insect communities and roost selection by western long-eared myotis* (*Myotis evotis*) *in Mesa Verde National Park, Colorado*. M.S. Thesis. Colorado State University, Fort Collins, Colorado. 106 pp.

Snider, E.A., P.M. Cryan, and K.R. Wilson. 2013. Roost selection by western long-eared myotis (*Myotis evotis*) in burned and unburned piñon-juniper woodlands of southwestern Colorado. *Journal of Mammalogy* 94:640–649.

Solick, D.I., and R.M.R. Barclay. 2006a. Morphological differences among western long-eared myotis (*Myotis evotis*) populations in different environments. *Journal of Mammalogy* 87:1020–1026.

Solick, D.I., and R.M.R. Barclay. 2006b. Thermoregulation and roosting behavior of reproductive and non-reproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. *Canadian Journal of Zoology* 84:589–599.

Solick, D.I., and R.M.R. Barclay. 2007. Geographic variation in the use of torpor and roosting behavior of female western long-eared bats. *Journal of Zoology* (*London*) 272:358–366.

Solvesky, B.G., and C.L. Chambers. 2009. Roosts of Allen's lappet-browed bat in northern Arizona. *Journal of Wildlife Management* 73:677–682.

South Carolina Department of Natural Resources. 2005. South Carolina comprehensive wildlife conservation strategy 2005–2010. 848 pp. <*http://teaming.com/sites/default/files/South%20Carolina%20Wildlife%20Action%20Plan.pdf*>. Cited 5 September 2017.

South Carolina Department of Natural Resources. 2015. South Carolina's state wildlife action plan 2015. <http://www.dnr.sc.gov/swap/index.html>. Cited 5 September 2017.

South Dakota Game, Fish, and Parks. 2014. The South Dakota wildlife action plan. 583 pp. <*http://gfp.sd.gov/wildlife/management/plans/wildlife-action-plan.aspx*> Cited 5 September 2017.

Sparks, D.W., and J.R. Choate. 2000 Distribution, natural history, conservation status, and biogeography of bats in Kansas. Pages 173–228 *in* J.R. Choate, ed., *Reflections of a Naturalist, Papers Honoring Professor Eugene H. Fleharty*. Sternberg Museum of Natural History, Fort Hays State University, Fort Hays, Kansas.

Sparks, D.W., and E.W. Valdez. 2003. Food habits of *Nyctinomops macrotis* at a maternity roost in New Mexico, as indicated by analysis of guano. *Southwestern Naturalist* 48:132–135.

Stadelmann, B., L.-K. Lin, T.H. Kunz, and M. Ruedi. 2007. Molecular phylogeny of New World Myotis (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution* 43:32–48.

Stager, K.E.1939. Status of *Myotis velifer* in California, with notes on its life history. *Journal of Mammalogy* 20:225–228.

Stager, K.E. 1942. The cave bat as food of the California lyre snake. *Journal of Mammalogy* 32:92.

Stager, K.E. 1943a. California leaf-nosed bat trapped by desert shrub. *Journal of Mammalogy* 24:396.

Stager, K.E. 1943b. Remarks on *Myotis occultus* in California. *Journal of Mammalogy* 24:197–199.

Steffen, B.J., T.L.Y. Osborne, T.C. Carter, and G.A. Feldhamer. 2006. The first record of the eastern small-footed myotis (*Myotis leibii*) in Illinois. *Transactions of the Illinois Academy of Science* 99:87–89.

Stephens, F. 1906. *California Mammals*. West Coast Publishing Company, San Diego, California. 351pp.

Stephens, T.C. 1945. Say's bat in Nebraska. *Journal of Mammalogy* 26:92.

Stevenson, C.L. 2008. *Availability and seasonal use of diurnal roosts by Rafinesque's big-eared bat and southeastern myotis in bottomland hardwoods of Mississippi*. M.S. Thesis. Mississippi State University, Starkville, Mississippi. 109 pp.

Stock, A.D. 1970. Notes on mammals of southwestern Utah. *Journal of Mammalogy* 51:429–433.

Storz, J.F. 1995. Local distribution and foraging behavior of the spotted bat (*Euderma maculatum*) in northwestern Colorado and adjacent Utah. *Great Basin Naturalist* 55:78–83.

Storz, J.F., and C.F. Williams. 1996. Population structure of subalpine bats in Colorado. *Southwestern Naturalist* 41:322–324.

Straney, D.O., M.H. Smith, R.J. Baker, and I.F. Greenbaum. 1976. Biochemical variation and genic similarity of *Myotis velifer* and *Macrotus californicus*. *Comparative Biochemistry and Physiology* 54B: 243–248.

Streicker, D.G., A.S. Turmelle, M.J. Vonhof, I.V. Kuzmin, G.F. McCracken, and C.E. Rupprecht. 2010. Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. *Science* 329:676–679.

Studier, E.H. 1968. Fringe-tailed bat in northeast New Mexico. *Southwestern Naturalist* 13:362.

Studier, E.H., and M.J. O'Farrell. 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae): I. Thermoregulation. *Comparative Biochemistry and Physiology* 41A:567–595.

Studier, E.H., V.I. Lysengen, and M.J. O'Farrell. 1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae): II. Bioenergetics of pregnancy and lactation. *Comparative Biochemistry and Physiology* 44A:467–471.

Stuemke, L.A., C.E. Comer, M.L. Morrison, W.C. Conway, and R.W. Maxey. 2014. Roosts of Rafinesque's big-eared bats and southeastern myotis in East Texas. *Southeastern Naturalist* 13 (Special Issue 5): 159-171.

Sutter, J.V., M.E. Andersen, K.D. Bunnell, M.F. Canning, A.G. Clark, D.E. Dolsen, and F.P. Howe. 2005. *Utah Comprehensive Wildlife Conservation Strategy*. Utah Division of Wildlife Resources Publication Number 05–19, Salt Lake City, Utah. 281 pp. <*https://dwrutahbats.nr.utah.gov/batbase_folders//public_documents/General/10–01–21_utah_cwcs_strategy.pdf* >. Cited 5 September 2017.

Suttkus, R.D., G.H. Clemmer, and C. Jones. 1978. Mammals of the riparian region of the Colorado River in the Grand Canyon area of Arizona. *Occasional Papers Tulane University Museum of Natural History* 2:1–23.

Swenk, M.H. 1908. A preliminary review of the mammals of Nebraska. *Studies from the Zoological Laboratory, University of Nebraska and the Nebraska Academy of Sciences* 89:5–88.

Swenson, J.E., and G.F. Shanks, Jr. 1979. Noteworthy records of bats from northeastern Montana. *Journal of Mammalogy* 60:650–652.

Szewczak, J.M., S.M. Szewczak, M.L. Morrison, and L.S. Hall. 1998. Bats of the White and Inyo Mountains of California-Nevada. *Great Basin Naturalist* 58:66–75.

Tamsitt, J.R., and D. Valdivieso. 1966. Parturition in the red fig-eating bat, *Stenoderma rufum*. *Journal of Mammalogy* 47:352–353.

Taylor, D.A.R. 2007. Water for wildlife: helping western bats find a place to drink. *Bats* 25:11–13.

Tennessee Wildlife Resources Agency. 2005. Tennessee's comprehensive wildlife conservation strategy. 231 pp. <*http://teaming.com/sites/default/files/Tennessee%20Wildlife%20Action%20Plan.pdf*> Cited 5 September 2017.

Tennessee Wildlife Resources Agency. 2015. Tennessee 2015 state wildlife action plan. 506 pp. <*http://www.tnswap.com/swap.cfm*>. Cited 5 September 2017.

Texas Parks and Wildlife. 2012. Texas conservation action plan: species of greatest conservation need. <*http://tpwd.texas.gov/huntwild/wild/wildlife_diversity/nongame/tcap/sgcn.phtml*>. Cited 5 September 2017.

Texas Parks and Wildlife. 2015. Nongame and rare species program: federal and state listed mammal species. <*https://tpwd.texas.gov/huntwild/wild/wildlife_diversity/nongame/listed-species/*>. Cited 5 September 2017.

Texas Parks and Wildlife. 2017. Fungus that causes white-nose syndrome in bats detected in Texas. Texas Parks and Wildlife Press Release from 23 March 2017. <*https://tpwd.texas.gov/newsmedia/releases/?req=20170323c*>. Cited 5 September 2017.

Thies, M.L., and K.M. Thies. 1997. Organochlorine residues in bats from Eckert James River Cave, Texas. *Bulletin of Environmental Contamination and Toxicology* 58:673–680.

Thomas, D.W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* 52:619–626.

Thomas, H.H., P.R. Moosman, Jr., J.P. Veilleux, and J. Holt. 2012. Foods of bats (Family Vespertilionidae) at five locations in New Hampshire and Massachusetts. *Canadian Field-Naturalist* 126:117–124.

Thompson, J., and K. Bay. 2012. Post-construction fatality surveys for the Dry Lake II Wind Project, Iberdrola Renewables, LLC February 2011: February 2012: Contract Report, 108 pp. <*ftp://50–201–198–131–static.hfc.comcastbusiness.net/DesertSun/Thompson%20and%20Bay_Dry%20Lake%20II%20Fatality%20Surveys%202011–2012_WEST%202012.pdf*>. Cited 21 December 2014.

Thomson, S.C., A.P. Brooke, and J.R. Speakman. 1998. Diurnal activity in the Samoan flying fox, *Pteropus samoensis*. *Philosophical Transactions of the Royal Society of London B* 353:1595–1606.

Thomson, S.C., A.P. Brooke, and J.R. Speakman. 2002. Soaring behaviour in the Samoan flying fox (*Pteropus samoensis*). *Journal of Zoology* (*London*) 256:55–62.

Thomson, T. 2013. *Roost ecology of eastern small-footed bats* (*Myotis leibii*) *in the southern Appalachian Mountains*. M.S. Thesis. Indiana State University. 75 pp.

Tibbitts, T., A. Pate, Y. Petryszyn, and B. Barns. 2002. Determining foraging and roosting areas for Underwood's mastiff bat (*Eumops underwoodi*) using radiotelemetry, at Organ Pipe Cactus National Monument, Arizona: Final summary Report, Year 2, Appendix G, Ecological Monitoring Program Report, 1997–2005. Organ Pipe Cactus National Monument, Ajo, Arizona. 14 pp. <*https://www.nps.gov/orpi/learn/nature/upload/EumopsFinal02.pdf*>. Cited 5 September 2017.

Tibbitts, T., and A. Pate. 2009. Cactus bats. *Bats* 27:3.

Timm, R.M., and H.H. Genoways. 2004. The Florida bonneted bat, *Eumops floridanus* (Chiroptera: Molossidae): distribution, morphometrics, systematics, and ecology. *Journal of Mammalogy* 85:852–865.

Tinkle, D.W., and W.W. Milstead. 1960. Sex ratios and population density in hibernating *Myotis*. *American Midland Naturalist* 63:327–334.

Tinkle, D.W., and I.G. Patterson. 1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. *Journal of Mammalogy* 46:612–633.

Tipps, T.M. 2012. *Morphological and molecular variation in Townsend's big-eared bat* (*Corynorhinus townsendii*) *in West Texas*. M.S. Thesis. Angelo State University. 35 pp.

Tobin, A. 2016. *Temporal scale moderates acceptance of gate design for bats at abandoned mines in the western United States*. M.S. Thesis. Northern Arizona University, Flagstaff, Arizona. 106 pp.

Tobin, A., and C.L. Chambers. 2017. Mixed effects of gating subterranean habitat on bats—a review. *Journal of Wildlife Management* 81:1149–1160.

Trejo-Salazar, R.E., E. Scheinvar., and L.E. Eguiarte. 2015. ¿Quién poliniza realmente los agaves? Diversidad de visitantes florales en 3 especies de *Agave* (Agavoideae: Asparagaceae). *Revista Mexicana de Biodiversidad* 86:358–369.

Trombulak, S.C., P.E. Higuera, and M. DesMeules. 2001. Population trends of wintering bats in Vermont. *Northeastern Naturalist* 8:51–62.

Trousdale, A.W. 2011. Ecology of tree-roosting Rafinesque's big eared bats in the eastern United States. Pages 27–38 *in* Loeb, S.C., M.J. Lacki, and D.A. Miller, eds., *Conservation and Management of Eastern Big-Eared Bats: A Symposium*. General Technical Report SRS–145. U.S. Department of Agriculture Forest Service, Asheville, North Carolina.

Trousdale, A.W., and D.C. Beckett. 2004. Seasonal use of bridges by Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, in southern Mississippi. *Southeastern Naturalist* 3:103–112.

Trousdale, A.W., and D.C. Beckett. 2005. Characteristics of tree roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in southeastern Mississippi. *American Midland Naturalist* 154:442–449.

Trousdale, A.W., D.C. Beckett, and S.L. Hammond. 2008. Short-term roost fidelity of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) varies with habitat. *Journal of Mammalogy* 89:477–484.

Tumlinson, R. 1993. Geographic variation in the lappet-eared bat, *Idionycteris phyllotis*, with descriptions of subspecies. *Journal of Mammalogy* 74:412–421.

Tumlinson, R., and M.E. Douglas. 1992. Parsimony analysis and the phylogeny of the plecotine bats (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 73:276–285.

Turner, G.G., D.M. Reeder, and J.T.H. Coleman. 2011. A five-year assessment of mortality and geographic spread of white-nose syndrome in North American bats and a look to the future. *Bat Research News* 52:13–27.

Turner, R.W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. *University of Kansas Muse-*

um of Natural History Miscellaneous Publication 60:1–178.

Turner, R.W., and J.K. Jones, Jr. 1968. Additional notes on bats from western South Dakota. *Southwestern Naturalist* 13:444–458.

Tuttle, M.D. 1964. *Myotis subulatus* in Tennessee. *Journal of Mammalogy* 45:148–149.

Tuttle, M.D., and L.R. Heaney. 1974. Maternity habits of *Myotis leibii* in South Dakota. *Bulletin of the Southern California Academy of Sciences* 73:80–83.

Tuttle, M.D., and D. Stevenson. 1982. Growth and survival of bats. Pages 105–150 *in* T.H. Kunz, ed., *Ecology of Bats.* Plenum Publishing Company, New York, New York.

Twedt, D.J., and C.R. Loesch. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. *Journal of Biogeography* 26:1215–1224.

Twente, J.W. 1954. Predation on bats by hawks and owls. *Wilson Bulletin* 66:135–136.

Twente, J.W. 1955a. Aspects of a population study of cavern-dwelling bats. *Journal of Mammalogy* 36: 379–390.

Twente, J.W. 1955b. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology* 36:706–732.

Twente, J.W. 1960. Environmental problems involving the hibernating bats in Utah. *Proceedings of the Utah Academy of Sciences, Arts and Letters* 37:67–71.

Udall, S.L. 1967. Office of the Secretary, native fish and wildlife, endangered species. *Federal Register* 32 (48):6.

U.S. Fish and Wildlife Service. 1976. 50 CFR Part 17. Endangered and threatened wildlife and plants; determination that two species of butterflies are threatened species and two species of mammals are endangered species. *Federal Register* 41:17736–17740.

U.S. Fish and Wildlife Service. 1979. 50 CFR Part 17. Endangered and threatened wildlife and plants; listing of Virginia and Ozark big-eared bats as endangered species, and critical habitat determination. *Federal Register* 44:69206–69208.

U.S. Fish and Wildlife Service. 1984. 50 CFR Part 17. Endangered and threatened wildlife and plants; determination of endangered status for seven birds and two bats of Guam and the Northern Mariana Islands. *Federal Register* 49:33881–33885.

U.S. Fish and Wildlife Service. 1988. 50 CFR Part 17. Endangered and threatened wildlife and plants; determination of endangered status for two long-nosed bats. *Federal Register* 53:38456–38460.

U.S. Fish and Wildlife Service. 1994. 50 CFR Part 17. Endangered and threatened wildlife and plants; animal candidate review for listing as endangered or threatened species. *Federal Register* 59:58982–59028.

U.S. Fish and Wildlife Service. 1996a. 50 CFR Part 17. Endangered and threatened species, plant and animal taxa: proposed rule. *Federal Register* 61:7596–7613.

U.S. Fish and Wildlife Service. 1996b. 50 CFR Part 17. Endangered and threatened species, plant and animal taxa: Notice of final decision on identification of candidates for listing as endangered or threatened. *Federal Register* 61:7595–7613.

U.S. Fish and Wildlife Service. 2005. 50 CFR Part 17. Endangered and threatened wildlife and plants; Mariana fruit bat (*Pteropus mariannus mariannus*): reclassification from endangered to threatened in the territory of Guam and listing as threatened in the Commonwealth of the Northern Mariana Islands. *Federal Register* 70:1190–1210.

U.S. Fish and Wildlife Service. 2011. 50 CFR Part 17. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the eastern small-footed bat and the northern long-eared bat as threatened or endangered. *Federal Register* 76:38095–38106.

U.S. Fish and Wildlife Service. 2013a. 50 CFR Part 17. Endangered and threatened wildlife and plants; endangered species status for the Florida bonneted bat; final rule. *Federal Register* 78:61004–61042.

U.S. Fish and Wildlife Service. 2013b. 50 CFR Part 17. Endangered and threatened wildlife and plants; 12–month finding on a petition to list the eastern small-footed bat and the northern long-eared bat as endangered or threatened species. *Federal Register* 78:61,046–61,080.

U.S. Fish and Wildlife Service. 2015a. 50 CFR Part 17. Endangered and threatened wildlife and plants; endangered status for 16 species and threatened status for 7 species in Micronesia. *Federal Register* 80:59424–59497.

U.S. Fish and Wildlife Service. 2015b. 50 CFR Part 17. Endangered and threatened wildlife and plants; threatened species status for the northern long-eared bat with 4(d) rule; final rule and interim rule. *Federal Register* 80:17974–18033.

U.S. Fish and Wildlife Service. 2016. 50 CFR Part 17. Endangered and threatened wildlife and plants; endangered status for five species from American Samoa. *Federal Register* 81:65466–18033.

U.S. Fish and Wildlife Service. 2017. 50 CFR Part 17. Endangered and threatened wildlife and plants; removal of the lesser long-nosed bat from the federal list of endangered and threatened wildlife. *Federal Register* 82:1665–1676.

U.S. Forest Service. 2005a. Forest Service Sensitive Species that are Not Listed or Proposed Under the ESA. U.S. Forest Service Report, Washington, D.C. 71 pp. <https://www.fs.fed.us/biology/resources/pubs/tes/fs_ss_1dec04.pdf>. Cited 5 September 2017.

U.S. Forest Service. 2005b. Forest Service Sensitive Species Summary. U.S. Forest Service Report, Washington D.C. 2 pp. <*https://www.fs.fed.us/biology/resources/pubs/tes/ss_sum_by_region_31Oct2005_fs.pdf*>. Cited 5 September 2017.

U.S. Forest Service. 2017. Caving rules. U.S. Forest Service, White River National Forest, Glenwood Springs, Colorado. <*https://www.fs.usda.gov/detail/whiteriver/home/?cid=stelprdb5363948*>. Cited 5 September 2017.

U.S. Geological Survey. 2015. Quarterly wildlife mortality reports. U.S. Geological Survey Online Reporting System. <*https://www.nwhc.usgs.gov/publications/quarterly_reports/index.jsp*>. Cited 5 September 2017.

U.S. Geological Survey. 2017. North American bat ranges, National Atlas of the United States, 1997–2014 edition. <*https://catalog.data.gov/dataset/north-american-bat-ranges-direct-download*>. Cited 26 September 2017.

U.S. Government Printing Office. 2000, Public Law 106–553 106th Congress. U.S. Government Printing Office, Washington, D.C. <*https://www.gpo.gov/fdsys/pkg/STATUTE-114/pdf/STATUTE-114–Pg2762.pdf*>. Cited 5 September 2017.

Utah Division of Wildlife Resources. 2015. Utah wildlife action plan. Utah Division of Wildlife Resources Report (Draft 2.0), Salt Lake City, Utah. 385 pp. <*http://wildlife.utah.gov/wap/wap2015draft2.pdf*>. Cited 5 September 2017.

Utzurrum, R.C.B., G.J. Wiles, A.P. Brooke, and D.J. Worthington. 2003. Count methods and population trends in Pacific island flying foxes. Pages 49–61 *in* T.J. O'Shea and M.A. Bogan, eds., *Monitoring Bat Populations in the United States and Territories: Problems and Prospects*. U.S. Geological Survey Information Technology Report ITR 2003–003.

Utzurrum, R.C.B, J.O. Seamon, and S.K. Schletz. 2006. A comprehensive strategy for wildlife conservation in American Samoa. Department of Marine and Wildlife Resources Report, Pago Pago, American Samoa. 116 pp. <http://teaming.com/sites/default/files/American%20Samoa%20SWAP.pdf >. Cited 5 September 2017.

Valdez, E.W. 2006. *Geographic variation in morphology, diet, and ectoparasites of Myotis occultus in New Mexico and southern Colorado*. Ph.D. Dissertation, University of New Mexico. 99 pp.

Valdez, E.W., and M.A. Bogan. 2009. Does variation in cranial morphology of *Myotis occultus* (Chiroptera: Vespertilionidae) reflect a greater reliance on certain prey types? *Acta Chiropterologica* 11:443–450.

Valdez, E.W., J.R. Choate, M.A. Bogan, and T.L. Yates. 1999a. Taxonomic status of *Myotis occultus*. *Journal of Mammalogy* 80:545–552.

Valdez, E.W., J.N. Stuart, and M.A. Bogan. 1999b. Additional records of bats from the Middle Rio Grande Valley, New Mexico. *Southwestern Naturalist* 44:398–400.

Valdez, E.W., C.M. Ritzi, and J.O. Whitaker, Jr. 2009. Ectoparasites of the occult bat, *Myotis occultus* (Chiroptera: Vespertilionidae). *Western North American Naturalist* 69:364–370.

Valdez, E.W., G.J. Wiles, and T.J. O'Shea. 2011. Diets of the sympatric Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*) and Mariana swiftlet (*Aerodramus bartschi*) on Aguiguan, Mariana Islands. *Pacific Science* 65:301–309.

Valiente-Banuet, A., M. Del Coro Arizmendi, A. Rojas-Martinez, and L. Dominguez-Canseco. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical*

Ecology 12:103–119.

Van Den Bussche, R.A., D.N. Lee, M.E. Judkins, J.E. Dyer, D.M. Thompson, R.C. Stark, W.L. Puckette, and B. Fuller. 2016. Molecular dietary analysis of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*). *Acta Chiropterologica* 18:181–191.

Van Zyll de Jong, C.G. 1984. Taxonomic relationships of Nearctic small-footed bats of the *Myotis leibii* group (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 62:2519–2526.

Van Zyll de Jong, C.G. 1985. *Handbook of Canadian Mammals*. National Museum of Natural Sciences, Ottawa, Ontario. 212 pp.

Van Zyll de Jong, C.G., and D.W. Nagorsen. 1994. A review of the distribution and taxonomy of *Myotis keenii* and *Myotis evotis* in British Columbia and the adjacent United States. *Canadian Journal of Zoology* 72:1069–1078.

Vaughan, T.A. 1954. Mammals of the San Gabriel Mountains of California. *University of Kansas Publications, Museum of Natural History* 7:513–582.

Vaughan, T.A. 1959. Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. *University of Kansas Publications Museum of Natural History* 12:1–153.

Vaughan, T.A. 1966. Morphology and flight characteristics of molossid bats. *Journal of Mammalogy* 47: 249–260.

Vaughan, T.A. 1980. Opportunistic foraging by two species of *Myotis*. *Journal of Mammalogy* 61:118–119.

Veilleux, J.P. 2007. A noteworthy hibernation record of *Myotis leibii* (eastern small-footed bat) in Massachusetts. *Northeastern Naturalist* 14: 501–502.

Vermont Fish and Wildlife Department. 2015. Endangered and threatened animals of Vermont. 3 pp. <*http://www.vtfishandwildlife.com/common/pages/DisplayFile.aspx?itemId=268519*>. Cited 5 September 2017.

Verts, B.J., and L.N. Carraway. 1998. *Land Mammals of Oregon*. University of California Press, Berkeley, California. 668 pp.

Virginia Department of Game and Inland Fisheries. 2005. Virginia's comprehensive wildlife conservation strategy. 36 pp. <*http://leg5.state.va.us/reg_agent/frmView.aspx?Viewid=62dc1002090~1&typ=40&actno= 002090&mime=application/pdf*>. Cited 5 September 2017.

Virginia Department of Game and Inland Fisheries. 2015a. Special legal status faunal species in Virginia. 20 pp. <*https://www.dgif.virginia.gov/wp-content/uploads/virginia-threatened-endangered-species.pdf*>. Cited 5 September 2017.

Virginia Department of Game and Inland Fisheries. 2015b. Virginia's 2015 wildlife action plan. 1,135 pp. <*http://bewildvirginia.org/wildlife-action-plan/pdf/2015–Virginia-Wildlife-Action-Plan.pdf*>. Cited 5 September 2017.

Voigt, C.C., and Y. Winter. 1999. Energetic cost of hovering flight in nectar-feeding bats (Phyllostomidae: Glossophaginae) and its scaling in moths, birds and bats. *Journal of Comparative Physiology B* 169: 38–48.

Von Bloeker, J.C., Jr. 1932. Summer records of *Eumops californicus* (Merriam). *Journal of Mammalogy* 13:274.

Von Bloeker, J.C., Jr. 1967. The land mammals of the Southern California Islands. Pages 245–264 *in* R.N. Philbrick, ed., *Proceedings of the Symposium on the Biology of the California Islands*. Santa Barbara Botanic Garden, Santa Barbara, California.

Vonhof, M.J., and R.M.R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74:1797–1805.

Vonhof, M.J., and R.M.R. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. *Journal of Wildlife Management* 61:674–684.

Vonhof, M.J., A.L. Russell, and C.M. Miller-Butterworth. 2015. Range-wide genetic analysis of little brown bat (*Myotis lucifugus*) populations: estimating the risk of spread of white-nose syndrome. *PLoS ONE* 10:e0128713. 23 pp.

Vorhies, C.T. 1935. The Arizona specimen of *Euderma maculatum*. *Journal of Mammalogy* 16:224–226.

Wainwright, J.M., and N.D. Reynolds. 2013. Cave hibernaculum surveys of a Townsend's big-eared bat (*Corynorhinus townsendii*) colony at Mount St. Helens, Washington. *Northwestern Naturalist* 94:

240–244.

Wai-Ping, V., and M.B. Fenton. 1989. Ecology of spotted bat (*Euderma maculatum*) roosting and foraging behavior. *Journal of Mammalogy* 70:617–622.

Waldien, D.L., and J.P. Hayes. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. *Northwest Science* 75:307–314.

Waldien, D.L., Hayes, J.P., and Arnett, E.B. 2000. Day-roosts of female long-eared myotis in western Oregon. *Journal of Wildlife Management* 64:785–796.

Walker, C.W., J.K. Sandel, R.L. Honeycutt, and C. Adams. 1986. Winter utilization of box culverts by vespertilionid bats in southeast Texas. *Texas Journal of Science* 48:166–168.

Walker, F.M., J.T. Foster, K.P. Drees, and C.L. Chambers. 2014. Spotted bat (*Euderma maculatum*) microsatellite discovery using illumina sequencing. *Conservation Genetics Resources* 6:457–459.

Warner, R.M. 1985. Interspecific and temporal dietary variation in an Arizona bat community. *Journal of Mammalogy* 66:45–51.

Warner, R.M., and N.J. Czaplewski. 1984. *Myotis volans*. *Mammalian Species* (224):1–4.

Warren, E.R. 1942. *The Mammals of Colorado: Their Habits and Distribution*. University of Oklahoma Press, Norman, Oklahoma. 330 pp.

Washington Department of Fish and Wildlife. 2015a. Washington state species of concern list. <http://wdfw.wa.gov/conservation/endangered/All/>. Cited 5 September 2017.

Washington Department of Fish and Wildlife. 2015b. Washington's state wildlife action plan: 2015 update. 1,095 pp. <*http://wdfw.wa.gov/publications/01742/wdfw01742.pdf*>. Cited 5 September 2017.

Washington Department of Fish and Wildlife. 2017. White-nose syndrome. <*http://wdfw.wa.gov/conservation/health/wns/*>. Cited 5 September 2017.

Watkins, L.C. 1977. *Euderma maculatum*. *Mammalian Species* (77):1–4.

Watkins, L.C., J.K. Jones, Jr., and H.H. Genoways. 1972. Bats of Jalisco, Mexico. *Special Publications of the Museum, Texas Tech University* 1:1–44.

Webb, O.L., and J.K. Jones, Jr. 1952. An annotated checklist of Nebraskan bats. *University of Kansas Publications, Museum of Natural History* 5:269–279.

Weller, T.J. 2008. Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest. *Biological Conservation* 141:2279–2289.

Weller, T.J., and C.J. Zabel. 2001. Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management* 65:489–497.

Weller, T.J., P.M. Cryan, and T.J. O'Shea. 2009. Broadening the focus of bat conservation and research in the USA for the 21st century. *Endangered Species Research* 8:129–145.

Weller, T.J., S.A. Shonene, T.J. Rodhouse, P.C. Ormsbee, and J.M. Zinck. 2007. Field identification of the cryptic vespertilionid bats, *Myotis lucifugus* and *M. yumanensis*. *Acta Chiropterologica* 9:133–147.

Weller, T.J., S.C. Thomas, and J.A. Baldwin. 2014. Use of long-term opportunistic surveys to estimate trends in abundance of hibernating Townsend's big-eared bats. *Journal of Fish and Wildlife Management* 5:59–69.

Wenner, A.S. 1984. Current status and management of gray bat caves in Jackson County, Florida. *Florida Field Naturalist* 12:1–24.

West Virginia Division of Natural Resources. 2015. 2015 State wildlife action plan. 106 pp. <*http://www.wvdnr.gov/2015%20West%20Virginia%20State%20Wildlife%20Action%20Plan%20Submittal.pdf*>. Cited 5 September 2017.

Whitaker, J.O., Jr., and N. Wilson. 1974. Host and distribution lists of mites (Acari), parasitic and phoretic, in the hair of wild mammals of North America, north of Mexico. *American Midland Naturalist* 91: 1–67.

Whitaker, J.O., Jr., and D.A. Easterla. 1975. Ectoparasites of bats from Big Bend National Park, Texas. *Southwestern Naturalist* 20:241–254.

Whitaker, J.O., Jr., and J.O. Douglas. 2006. Bat rabies in Indiana. *Journal of Wildlife Management* 70:1569–1573.

Whitaker, J.O., Jr., and W.J. Hamilton, Jr. 1998. *Mammals of the Eastern United States.* Comstock Publishing, Ithaca, New York. 583 pp.

Whitaker, J.O., Jr., M. Brooks, L. Scott, L.S. Finn, and C.L. Smith. 2007. Food habits of Rafinesque's big-eared bat from Florida. *Florida Scientist* 70:202–206.

Whitaker, J.O., Jr., C. Maser, and L.E. Keller. 1977. Food habits of bats in western Oregon. *Northwest Science* 51:46–55.

Whitaker, J.O., Jr., C. Maser, and S.P. Cross. 1981. Food habits of eastern Oregon bats, based on stomach and scat analyses. *Northwest Science* 55:281–292.

Whitby, M., S. Bergeson, T. Carter, S. Rutan, and R. McClanahan. 2013. The discovery of a reproductive population of eastern small-footed bat, *Myotis leibii*, in southern Illinois using a novel survey method. *American Midland Naturalist* 169:229–233.

White, C.M., D.J. Brimm, and F. Clunie. 1988. A study of peregrines in the Fiji Islands, South Pacific Ocean. Pages 275–288 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds., *Peregrine Falcon Populations: Their Management and Recovery*. The Peregrine Fund, Boise, Idaho.

Wiederholt, R., L. López-Hoffman, J. Cline, R.A. Medellín, P. Cryan, A. Russell, G. McCracken, J. Diffendorfer, and D. Semmens. 2013. Moving across the border: modeling migratory bat populations. *Ecosphere* 4:1–16.

Wiles, G.J. 1992. Recent trends in the fruit bat trade on Guam. Pages 53–60 *in* D.E. Wilson and G.L. Graham, eds., *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference.* United States Fish and Wildlife Service Biological Report 90.

Wiles, G.J., T.J. O'Shea, D.J. Worthington, J.A. Esselstyn, and E.W. Valdez. 2011. Status and natural history of *Emballonura semicaudata rotensis* on Aguiguan, Mariana Islands. *Acta Chiropterologica* 13: 299–309.

Williams, D.F., J.D. Druecker, and H.L. Black. 1970. The karyotype of *Euderma maculatum* and comments on the evolution of the plecotine bats. *Journal of Mammalogy* 51:602–606.

Williams, J.A., M.J. O'Farrell, and B.R. Riddle. 2006. Habitat use by bats in a riparian corridor of the Mojave Desert in southern Nevada. *Journal of Mammalogy* 87:1145–1153.

Willis, C.K.R., and R.M. Brigham. 2004. Roost switching, roost sharing, and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behavior* 68:495–505.

Wilson, D.E., and J. Engbring. 1992. The flying fox *Pteropus samoensis* and *Pteropus tonganus*: status in Fiji and Samoa. Pages 74–101 *in* D.E. Wilson and G.L. Graham, eds., *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference.* United States Fish and Wildlife Service Biological Report 90.

Wilson, J.M., and R.M.R. Barclay. 2006. Consumption of caterpillars by bats during an outbreak of western spruce budworm. *American Midland Naturalist* 155:244–249.

Wolf, S.A., and W.W. Shaw. 2002. Roost selection of bridges by bats. Arizona Game and Fish Department, Heritage Program Report Grant U98007, Phoenix, Arizona. 290 pp. <*http://azmemory.azlibrary.gov/cdm/ref/collection/statepubs/id/16648*>. Cited 5 September 2017.

Wolters, M.S., and C.O. Martin. 2011. Observations of parturition in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) beneath a concrete bridge. *Southeastern Naturalist* 10:178–180.

Woodsworth, G.C. 1981. *Spatial partitioning by two species of sympatric bats, Myotis californicus and Myotis leibii.* M.S. Thesis. Carleton University. 68 pp.

Woodsworth, G.C., G.P. Bell, and M.B. Fenton. 1981. Observations of the echolocation, feeding behavior, and habitat use of *Euderma maculatum* (Chiroptera: Vespertilionidae) in south central British Columbia. *Canadian Journal of Zoology* 59:1099–1102.

Worthington, D.J. 1991. *Abundance, distribution, and sexual segregation of bats in the Pryor Mountains of south central Montana*. M.A. Thesis. University of Montana. 41 pp.

Wyoming Game and Fish Department. 2017a. Wyoming state wildlife action plan. 1,692 pp. <https://wgfd.wyo.gov/Habitat/Habitat-Plans/Wyoming-State-Wildlife-Action-Plan >. Cited 5 September 2017.

Wyoming Game and Fish Department. 2017b. Species of greatest conservation need. <*https://wgfd.wyo.gov/WGFD/media/content/PDF/Habitat/SWAP/Wyoming-SGCN.pdf*>. Cited 5 September 2017.

Yancey, F.D. II. 1997. The mammals of Big Bend Ranch State Park, Texas. *Special Publications of the Muse-*

um, Texas Tech University 39:1–210.

Yates, D.E., E.M. Adams, S.E. Angelo, D.C. Evers, J. Schmerfeld, M.S. Moore, T.H., Kunz, T. Divoll, S.T. Edmonds, C. Perkins, R. Taylor, and N.J. O'Driscoll. 2014. Mercury in bats from the northeastern United States. *Ecotoxicology* 23:45–55.

Zanowiak, D.J., T.P. Harrison, and W. Caire. 1993. External bacteria of hibernating *Myotis velifer* (Chiroptera: Vespertilionidae). *Southwestern Naturalist* 38:73–76.

Zielinski, W.J., and S.T. Gellman. 1999. Bat use of remnant old-growth redwood stands. *Conservation Biology* 13:160–167.

Zielinski, W.J., M.J. Mazurek, and J. Zinck. 2007. Identifying the species of bats roosting in redwood basal hollows using genetic methods. *Northwest Science* 81:155–162.

Zimmerman, E. 1970. Additional records of bats from Utah. *Southwestern Naturalist* 15:263–264.

Zinck, J.M., D.A. Duffield, and P.C. Ormsbee. 2004. Primers for identification and polymorphism assessment of Vespertilionid bats in the Pacific Northwest. *Molecular Ecology Notes* 4:239–242.

Zinn, T.L., and S.R. Humphrey. 1981. Seasonal food resources and prey selection of the southeastern brown bat (*Myotis austroriparius*) in Florida. *Florida Scientist* 44:81–90.

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