

Patterns of Nest Occupancy and Provisioning in *Cerceris rufopicta* Smith (Hymenoptera: Sphecidae)

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Data are presented on prey choice, nest architecture, natural enemies, daily activity patterns, and seasonal patterns of nest occupancy in a population of Cerceris rufopicta Smith in northeastern Kansas. Most behaviors observed in this population are quite similar to those reported from populations in Florida, North Carolina, Pennsylvania, and New York. As in the eastern populations, by far the most common prey are two species of beetles in the subfamily Eumolpinae (Chrysomelidae), but late in the season at least one wasp began provisioning primarily with Eugnamptus angustatus. (Herbst), a weevil in the family Rhynchitidae, not previously recorded as prey of C. rufopicta. Nest architecture and natural enemies are very similar to what has been reported for the eastern populations, but provisioning activity in the Kansas population occupies a much greater part of the day, with some wasps continuing to provision even after sunset. This difference is not because individual wasps in Kansas are active for a longer period of time, but because the activity schedules of different individuals within the Kansas aggregation are not closely synchronized. Approximately half of the nests that were monitored over a period of three and a half weeks were occupied by a single wasp. Other nests changed ownership during the course of the study, either because the original owner disappeared and another wasp moved in, or because one wasp drove another away from a nest. During the time that ownership of a nest was being contested it might be simultaneously used by more than one wasp, but no evidence of cooperative joint nesting was seen in this population.

KEY WORDS: *Cerceris rufopicta*; nest usurpation; prey; natural enemies.

INTRODUCTION

Cerceris is the largest genus of wasps in the superfamily Apoidea (*sensu* Michener, 1986), with more than 850 species worldwide (Bohart and Menke, 1976).

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It includes a number of common and conspicuous species whose behavior and ecology have been studied at least in a general way. Adult females excavate relatively complex multicellular nests in the ground, usually in "bare soil of a firm nature" (Bohart and Menke, 1976). These nests are provisioned with beetles or bees that the female wasp captures and paralyzes with venom injected by her sting. A few species of *Cerceris* have attracted special attention from researchers interested in the evolutionary origins of social behavior, because two or more adult females simultaneously occupy a common burrow system, with each female apparently provisioning cells and ovipositing in them (Alcock, 1975, 1980; Elliott *et al.*, 1986; Evans and Hook, 1982a, b, 1986; Grandi, 1944; Hook, 1987; McCorquodale, 1988, 1989a; Salbert and Elliott, 1979; Tsuneki, 1947, 1965). Such nest sharing is uncommon in wasps in the superfamily Apoidea (see review by Matthews 1991), and a good deal of effort in recent years has been devoted to understanding the factors that favor the evolution of this behavior in *Cerceris* (references cited above, plus Elliott and Elliott, 1987; Elliott *et al.*, 1981; Evans, 1989; field, 1995; McCorquodale, 1989b, c, 1990; Willmer, 1985). However, not all species of *Cerceris* that have been studied are communal, and a more rigorous assessment of hypotheses about factors that favor the evolution of communal nesting in this genus requires a more detailed and comprehensive knowledge of nesting behavior in solitary as well as communal species. A basic requirement is the close monitoring of nests and wasps that have been clearly marked for individual recognition; at least some such information is currently available for 25 species (Matthews, 1991, Table 17.1). This paper presents data on patterns of nest use in a population of *Cerceris rufopicta* Smith, a species in which communal nesting has not been observed.

Cerceris rufopicta Smith is a fairly common species in the eastern and central United States, occurring from the east coast as far west as the extreme southwestern corner of South Dakota and the central parts of Nebraska, Kansas, and Texas (Scullen, 1965).³ Several brief studies have provided a basic overview of nest architecture, prey, and nest parasites of populations of *C. rufopicta* at a number of localities in the eastern United States: Florida (Krombein, 1964), North Carolina (Krombein, 1952, 1953); Pennsylvania (Kurczewski and Miller, 1984), and three localities in central New York (Evans, 1971; Kurczewski and Miller, 1984). Our research builds on these earlier studies by providing quantitative measures of daily activity schedules and long-term patterns of nest occupancy by individually marked females. It also provides comparative data on nest

³This species is referred to in the older literature, including most of the behavioral studies cited herein, as *Cerceris robertsonii* Fox. Scullen (1965) suggested that *C. robertsonii* and *C. rufopicta* might be synonyms, and Ferguson (1983) formally proposed the synonymy, with *C. rufopicta* having priority.

architecture and prey selection from a population in northeastern Kansas, far to the west of the populations studied by previous authors.

METHODS

The study was conducted at a site about 8 km east of Lawrence, Douglas County, Kansas, from June 22 to July 17, 1995. Numerous nests were located along and adjacent to a dirt road between a cultivated field and a riparian woodland bordering the Kansas River. The soil in this area was a well-compacted sandy clay that was very hard and firm when dry.

Each of us monitored the activity of wasps in half of a 5 × 5-m area in which we found 25 nests (although not all of these nests were active at the same time). We spent from 3 to 8 h each day observing and recording wasp activity (see Table IV for details), taking care to schedule observations evenly throughout the day, from 0820 to 2115. One of us (J.D.A.) also conducted more extensive observations for 2 consecutive days (12 h on July 5 and 11 h on July 6). Observations were canceled because of heavy rain on 3 days (June 25, 26, and 28), and the study area was inaccessible for 4 days (July 9–12) because of construction work on the only road leading to the site.

Thirty adult female wasps were marked for individual identification with two spots of color on the dorsum of the thorax, using Pentel Paint Pens (size 0.5). These wasps were originally selected for marking when we observed them entering burrows in the ground. Once a wasp was inside the nest, we placed an inverted transparent plastic cup over the entrance, so that we could capture her when she emerged. We found it helpful to keep these cups in place over the nest entrance except when a wasp (or nest parasite) was trying to enter or leave, because provisioning wasps would otherwise enter and leave nests too rapidly for us to see their individual paint markings. Other than slowing the wasps down enough to enable us to identify them accurately, these cups did not seem to seriously disrupt the wasps' behavior. A wasp would quickly enter the nest or fly away as soon as the glass was moved away from the nest entrance. Several other researchers (Evans and Hook, 1982a; Hook, 1987; McCorquodale, 1989a) have used clear plastic cups in a similar manner in their studies of other species of *Cerceris*.

The nest in which a wasp was captured was marked with a nail that was inserted into the ground near the nest entrance and painted with the same color pattern used for the wasp originally captured and marked as the nest. Having marked a nest, we recorded the identity of every wasp entering and leaving it, and whether or not she was carrying prey, as well as the time of day when each event occurred. In this paper, times of day are reported as Central Daylight Saving Time on a 24-h clock. Durations of various wasp activities will usually

be reported as minutes and tenths of a minute (e.g., 2 min and 30 s = 2.50 min) or as hours and tenths of an hour.

We also extracted 10 nests at various dates during the nesting season in order to study their structure and contents. Nest diagrams were drawn in the field, and tape measures and calipers were used to measure burrow and cell dimensions and depths of cells below the surface. Cell contents collected in the field were subsequently examined and inventoried in the laboratory with the aid of a stereomicroscope. In cells where some or all of the prey had been consumed, we inferred the number of prey by reassociating unconsumed parts of the exoskeleton. Although a few body parts were often missing, we consistently found that the number of elytra, metanota, metasterna, and/or pronota would match up and enable us to estimate confidently the number of prey in the cell. We also observed that the degree of disarticulation of consumed prey was consistently greater in cells that had a large *Cerceris* larva or cocoon than in cells with no immature wasp. We suspect that nest cells in which we found no immature *Cerceris*, but remains of prey that had been consumed but not completely disarticulated, had been cleptoparasitized by miltogrammine maggots.

Voucher specimens of *Cerceris rufopicta*, prey, and nest parasites are deposited in the collection of the Snow Entomology Division, Kansas University Natural History Museum (KUNHM), Lawrence. Identifications of beetle prey were provided by Dr. Donald Windsor of the Smithsonian Tropical Research Institute (Chrysomelidae) and by Dr. Robert Hamilton of Loyola University of Chicago (Rhynchitidae). *Cerceris rufopicta* was identified with the key and description in Scullen's (1965) revision of North American *Cerceris* and by comparison with KUNHM specimens that had been determined by Scullen. Nest parasites were identified by a similar process, using the following literature: Chrysididae—Bohart and Kimsey (1982), French (1982), and KUNHM specimens determined by L. D. French and R. M. Bohart; Mutillidae—Mickel (1924) and KUNHM specimens determined by D. Manley and C. E. Mickel; and Sarcophagoidae and Miltogramminae: Shewell (1987).

RESULTS

Daily Activity Pattern

Female wasps spend the night inside the nest, which they close from inside with a plug of soil when they have completed the day's provisioning. The first sign of activity the following morning is the removal of this soil plug from the entrance. We observed the time of day when a wasp first opened her nest on 41 occasions, and in 29 cases (71%) the nest had been opened by 0830. A few nests, however, had already been opened at the time of our first observations at 0820 h. Usually the wasp did not leave the nest immediately after unplugging

the entrance but remained just inside the entrance for some time before departing (mean duration for seven timed intervals = 29 min; range, 2–78 min).

The nest entrance usually remained open while a wasp was provisioning. One simple way to compare the hunting activities of individual wasps is to measure the durations of provisioning trips, defined as trips in which wasps were definitely seen to be carrying prey when she returned to her nest. In our study population, there were nine individuals who made at least three such trips on at least 3 days (more detailed activity records for these individuals are presented in the section on Patterns of Nest Occupancy.) For this group of wasps, the duration of a provisioning trip varied from 2.2 to 161.7 min (mean = 26.35 min, SD = 19.88 min; $N = 305$ trips). When calculated separately for each individual wasp (Table I), the mean duration of provisioning trips varied from 22.26 min (wasp BR) to 38.68 min (wasp WW). The variation in duration of provisioning trips by these individuals (as measured by sample standard error to take account of different sample sizes for different individuals) ranged from a low of 2.82 min (wasp BR) to a high of 9.03 min (wasp RO).

The time spent inside the nest between provisioning trips was also quite variable, ranging from 1 to 141 min (mean = 6.5 min, SD = 5.5 min; $N = 313$ bouts.) With our usual observation protocol, we rarely saw a wasp close the nest from inside after bringing in prey and then resume provisioning later on the same day. We recorded such behavior on only 12 of 355 occasions (3%) when a wasp returned to her nest, and the wasp remained inside the nest for an average of 152 min in these instances (range 14–356 min; SD = 102.8 min). The extended observations by J.D.A. on July 5 and 6 shed some light on the significance of these relatively rare events. Of the 10 wasps that provisioned nests on 1 or both of these days, 4 provisioned in a single continuous bout, whereas the other 6 provisioned in two distinct bouts separated by a period during which the nest was sealed from inside. The total amount of time spent provisioning each day did not differ between the two groups of wasps. The median duration of provisioning bouts was 6.05 h for wasps who provisioned in one bout and a combined total of 5.72 h for wasps who provisioned in two bouts (Mann–Whitney $U = 17$, NS). Each wasp seemed to follow her own idiosyncratic pattern of daily activity, making it relatively unlikely that our usual schedule of observations would coincide with the end of the first bout of provisioning and the start of the second for a wasp who provisioned in two bouts on a given day.

Within the nesting area, provisioning took place all through the day, from about 0800 (before 0820) to 2100 (last record, 2115). The average number of trips per hour showed two peaks, one between 1000 and 1200 and the other between 1400 and 1700 (Fig. 1). If one plots the average number of prey brought in per wasp per hour, one finds a generally similar but more irregular pattern, with the highest peak between 1700 and 1800 (Fig. 2). During the extended

Table I. Durations of Provisioning Trips, i.e., Trips when a Wasp was Definitely Seen to be Carrying Prey when She Returned to Her Nest. Durations and Associated Measures are in Minutes and Tenths of a Minute, as Explained in the Text.^{a,b}

	WASP											All Wasps
	RS	GrB	GoB	GrR	BR	WW	BGo	RO	GrO			
Total number (no.) of trips	56	49	45	39	36	28	27	15	10			305
No. of days seen provisioning	12	10	11	11	11	9	9	5	3			80
Minimum ^c no. trips/day	1	2	1	1	1	1	1	1	3			1
Maximum no. trips/day	12	7	7	7	7	7	7	6	4			12
No. of nests provisioned	1	1	1	1	2	1	2	1	1			11
Date of first provisioning	6/29	6/23	6/23	6/23	6/23	6/23	6/23	7/07	7/01			6/23
Date of last provisioning	7/17	7/08	7/08	7/06	7/08	7/08	7/08	7/17	7/14			7/17
Mean duration of trips	23.42	22.75	25.54	30.93	22.26	38.68	33.32	28.45	30.60			26.35
S.D. in duration of trips	25.90	24.37	28.78	17.51	16.90	20.53	31.62	34.97	12.41			19.88
S.E. in duration of trips	7.48	3.48	8.68	5.28	2.82	3.88	6.09	9.03	3.93			1.14
Minimum duration of trips	2.23	3.33	4.08	2.27	9.90	13.08	4.97	3.08	15.80			2.23
Maximum duration of trips	136.37	125.72	161.65	67.68	59.50	83.33	156.08	136.92	55.55			161.65

^aS.D. = standard deviation.

^bS.E. = standard error; dates presented as month/day (e.g., July 2 is 7/02).

^cExcluding days when wasp was not seen provisioning.

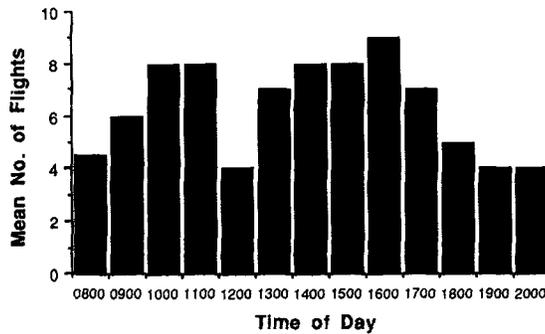


Fig. 1. Mean hourly number of returns to the nest at different times of day, based on observations of 19 individually marked female wasps. Intervals on the *x* axis are labeled according to the time of day at the start of the interval; e.g., 0800 refers to the interval 0800 to 0859.

observations on July 5 and 6, the number of prey brought to a nest by a wasp over the course of an entire day varied from 0 to 10 (median = 4 prey, *N* = 16 wasp days).

Wasps would sometimes continue their activities away from the nest until very late in the day. There were 19 occasions when we observed a wasp containing to bring prey to the nest after 2000. Some wasps continued activity away from the nest even after sunset, which occurred at about 2045. This is not to say that each wasp was active for this many hours each day. Again, our best information about how long an individual wasp was active on a given day comes from the prolonged observations on July 5 and 6. Ten of the monitored nests were active on these dates, five of them on both days. The number of hours that a wasp was active making trips to and from her nest ranged from 0.87 to 9.15 (mean = 4.92 h, SD = 2.38 h; *N* = 13 wasps days, excluding 3 wasp days for which accurate measurements were not obtained.)

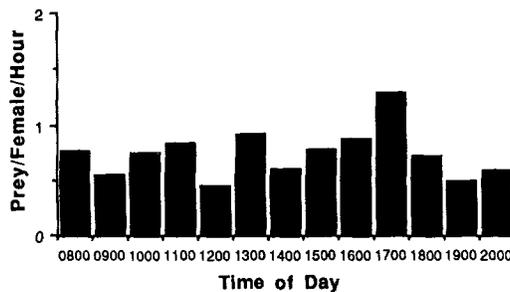


Fig. 2. Average number of prey brought in per female per hour at different times of day, based on observations of 19 individually marked female wasps. Time of day labeled as in Fig. 1.

It is also noteworthy that some wasps continued provisioning even under conditions such as strong winds and light rainfall, because such weather usually deters provisioning by many species of solitary wasps and bees.

Before closing the nest after bringing in the last prey of the day, a wasp often made another flight away from the nest. We observed the end of a day's activity on 38 occasions, and on 30 of these (79%), the female's final flight was a nonprovisioning trip. The duration of this final, nonprovisioning trip averaged 39.6 min (range, 7–113 min; $N = 26$ timed flights.)

Seasonal Activity Pattern

We suspect that the nesting season started shortly before we found the aggregation on June 21. The primary evidence for this is that we did not make any unequivocal observations of female wasps starting to excavate new nests after we began recording data on marked wasps, but we observed many fresh tumuli during the first few days when we were marking wasps and nests. Field (1995) has reported that he never observed *Cerceris arenaria* in England initiating nests by digging from the surface at the start of the season, and he suggested that the exit tunnels that wasps dug in emerging from their natal nests often became modified into nests. Perhaps *Cerceris rufopicta* initiates new nests in a similar manner. Another reason for suspecting that we found the nest aggregation near the start of the nesting season is that we observed males along the edges of the riparian woodland near the nesting area during these first days of the study. [Because many philanthine wasps are protandrous (Evans and O'Neill, 1988), the presence of males may indicate that our observations began near the start of the nesting season.] Heavy rains on June 25 and 26 washed the tumuli away from the nests we were monitoring. On subsequent days, we occasionally found when we arrived at the study area that a tumulus of fresh soil was present at a nest entrance that had not had such a tumulus when we left the previous evening. Our limited observations (fresh tumuli were recorded on six occasions) suggest that such tumuli do not necessarily indicate initiation of a new nest or a change in ownership of the nest. On four occasions, the wasp provisioning the nest at the time a fresh tumulus was recorded had been occupying that nest for several days previously and continued to occupy and provision it on subsequent days. One spot where a fresh tumulus was seen on July 5 seemed to represent a new nest, although provisioning activity only continued at that nest for 3 days after it was marked. Another nest that had a fresh tumulus on July 5 had just been newly occupied after a period of 4 days of inactivity.

We stopped recording data on wasp activity when only two nests showed any sign of being provisioned. One of these nests was excavated 2 days later, and the wasp that had been provisioning it was found dead in the main burrow at a depth of about 19 cm, below a plug of soil about 3 cm long. Occasional

visits to the site in later weeks showed no evidence of wasp activity, and the weedy vegetation bordering the road grew much taller and denser than it had been while wasps were actively provisioning nests. Consequently, we suspect that this population of *Cerceris rufopicta* is univoltine.

Nest Architecture

Ten nests were excavated during the course of the study: one on June 30, two on July 1, one on July 6, four on July 7, one on July 18, and one on July 19–20. The first nest to be excavated contained two cells. The last two nests, which contained 14 and 11 cells, respectively, had been monitored for several weeks, and provisioning had ceased one or 2 days before they were excavated.

The general structure of the nests in this population is similar to that of the populations of *Cerceris rufopicta* described by other authors (Krombein, 1952, 1953, 1964; Evans, 1971; Kurczewski and Miller, 1984) (data from all localities summarized in Table II). The nest (as illustrated in Evans, 1971) at our site consists of a nearly vertical burrow 13 to 40 cm in depth (mean = 20.22 cm, SD = 9.93 cm; $N = 10$), at the end of which are cell burrows (in the terminology of Evans and O'Neill, 1988) leading to the cells (mean cell burrow length = 6.44 cm, SD = 24.0 mm; $N = 18$). As a rule, the oldest cells in each nest were found at the greatest depth, with younger cells at progressively shallower depths [= regressive type of nest structure in the terminology of Iwata (1976)]. In three of the nests that we excavated, we found old cells with empty *Cerceris* cocoons, which suggests that at least some nests are "reactivated" from a previous generation.

Number and Identity of Prey

The number of prey found in cells ranged from 3 to 22 (mean = 7.75, SD = 3.52; $N = 56$ cells from 10 nests). Prey were also occasionally found within the main burrow, where they were presumably being stored temporarily, as has been reported previously for *C. rufopicta* (Krombein, 1952, 1953, 1964; Evans, 1971; Kurczewski and Miller, 1984) and for other species of *Cerceris* (Bohart and Menke, 1976). Our observations are consistent with the reports of previous authors that the prey are weakly paralyzed, sometimes even capable of walking (Krombein, 1952; Kurczewski and Miller, 1984), and that cells are mass provisioned (Krombein, 1952, 1964; Evans, 1971; Kurczewski and Miller, 1984). We excavated 12 cells that contained intact prey and a wasp egg and, thus, gave us an opportunity to measure the total wet weight of prey that an adult wasp provided for her offspring. The total wet weight per cell ranged from 72 to 284 mg (mean = 135 mg, SD = 62.7 mg), and the mean weight of an individual prey was 23.8 mg. All but three of these prey were *Fidia viucida* Walsh; the rest were *Rhaphiopterus praetextus* (Say).

Table II. Comparison of Nest Dimensions for *Cerceris rufopicta* from Several Localities. CI and CII Refer to Two Different Colonies Studied by Krombein at Kill Devil Hills, North Carolina. All Measurements are in Centimeters; Cell Depth is the Vertical Distance (to the Nearest Centimeter) from the Ground Surface to the Cell. We Show Minimum and Maximum Cell Depths Reported for Each Locality. Values Reported for Cell Length and Maximum Diameter are Means, with Range (if Available) Shown in Parentheses. Descriptions of Soil Types are Quoted Verbatim from the References Cited.

Locality	Number of nests	Cell depth	Cell length	Cell diameter	Soil type	Reference
Ithaca, NY	3	20-30	2.0	0.8	Coarse sandy gravel	Evans (1971)
Colonie, NY	1	25-27	not reported	not reported	Flat, fine-grained sand	Evans (1971)
Auburn, NY	3	17-24	1.4	0.82	Sand pits and blowouts	Kurczewski & Miller (1984)
Presque Isle State Park, PA	7	16-38	1.27	0.83	Sand pits and blowouts	Kurczewski & Miller (1984)
Kill Devil (CI)	3	23-51	(1.0-1.5)	(0.7-1.1)	Compacted sand	Krombein (1952)
Hills, NC (CII)	2	41	not reported	not reported	Compacted sand	Krombein (1953)
Lake Placid, FL	1	41-47	1.33	0.65	not reported	Krombein (1964)
Lawrence, KS	10	15-45	(1.2-1.4)	(0.5-0.8)	Compact, fine-grained sand	This study
			1.74	9.5		
			(1.2-2.2)	(0.7-1.1)		

In a sample of 296 prey identified from nest excavations, two species of eumolpine chrysomelid beetles were by far the most abundant: *Fidia viticida* (204 individuals, or 69% of all prey) and *Rhabdopterus praetextus* (50 individuals, or 17% of all prey). Another five specimens (2% of all prey) were other species of chrysomelids (two of these were intact: one was a eumolpine, the other a cryptocephaline). Two cells provisioned at a single nest during the final days of the study contained 37 individuals of *Eugnamptus angustatus* (Herbst), a rhynchitid weevil. These 37 specimens represent 12% of the total number of prey individuals found in nest excavations, but an individual of this weevil species is approximately half the mass of the two common species of chrysomelids used as prey. Most cells contained only a single species of beetle: 60% contained only *Fidia*, 12% contained only *Rhabdopterus*, 23% contained a mixture of *Fidia* and *Rhabdopterus*, and 5% (the two cells mentioned above) contained mostly weevils and one or two chrysomelids other than *Fidia* or *Rhabdopterus*. Several other studies have reported *Fidia viticida* and various species of *Rhabdopterus* as prey of *Cerceris rufopicta* (Table III), but this is the first record of weevils (Curculionoidea) being used as prey by this wasp.

Nest Parasites and Estimated Rates of Parasitism

We detected the presence of several potential nest parasites in the study area. On 12 occasions we recorded miltogrammine flies (Diptera: Sarcophagidae) inspecting nest entrances, and 4 of these flies entered the nest, remaining inside for 12 to 20 s. Two of these flies were collected as voucher specimens. One is a species of *Metopia* Meigen, collected on July 5 after spending 14 s inside a nest; the other is a species of *Phrosinella* Robineau-Desvoidy, collected on July 2 after spending 12 s inside a nest. We also observed miltogrammines pursuing female wasps carrying prey back to their nests on four occasions, and at least twice we saw the fly's abdomen contact the wasp's prey. These four flies were collected and identified as species of *Senotainia* Macquart *sensu* G. E. Shewell. The genera *Metopia*, *Phrosinella*, and *Senotainia* are common parasites of aculeate wasps (Evans and West Eberhard, 1970).

On eight occasions we saw chrysidid wasps inspecting nest entrances, and once we saw a chrysidid enter a nest. The latter wasp was collected and identified as a female of *Hedychrum confusum* Buysson, a species that has also been observed entering nests of *Cerceris halone* Banks in Virginia [(Byers, 1978); misidentified as *Hedychrum violaceum* Brullé according to French (1982)].

Twice we saw adult female mutillid wasps enter a *Cerceris* nest. On June 27, a mutillid entered nest F and remained inside for 63 s. This wasp was captured as she left the nest and later tentatively identified as *Pseudomethoca sanbornii* (Blake). Nest F was excavated on July 1 and found to contain five provisioned cells. Three cells had a *Cerceris* larva and two had a *Cerceris*

Table III. Prey Records for *Cerceris rufopicta* from Localities Described in Table I, Based on the References Cited Therein. Kurczewski and Miller (1984) did not Distinguish Between the New York and Pennsylvania Localities in Reporting Prey Records. Prey at the Lawrence, KS Site also Included Five Specimens of Chrysomelid Beetles that have not been Identified to Genus. Number in Parentheses Following each Locality Listing Shows the Percentage of all Specimens at that Locality Represented by that Species.

Prey	Locality
Eucnemidae	
<i>Deltometopus amoenicornis</i>	Auburn, NY/Presque Isle, PA (0.3%)
Chrysomelidae	
Eumolpinae	
<i>Colaspis brunnea</i>	Auburn, NY/Presque Isle, PA (24%)
<i>C. favosa</i>	Lake Placid, FL (98%)
<i>C. suilla</i>	Auburn, NY/Presque Isle, PA (3%)
<i>Fidia viticida</i>	Auburn, NY/Presque Isle, PA (19%)
	Lawrence, KS (69%)
<i>Metachroma angustulum</i>	Auburn, NY/Presque Isle, PA (0.3%)
<i>Paris</i> sp.	Lake Placid, FL (2%)
<i>Rhapdopterus picipes</i>	Ithaca, NY (100%)
	Kill Devil Hills, NC (50%)
<i>R. praetextus</i>	Lawrence, KS (17%)
<i>Tymnes tricolor</i>	Colonie, NY (100%)
	Auburn, NY/Presque Isle, PA (18%)
Cryptocephalinae	
<i>Cryptiocephalus notatus</i>	Kill Devil Hills, NC (49%)
<i>C. quadruplexus</i>	Auburn, NY/Presque Isle, PA (11%)
<i>Pachybrachis dilatatus</i>	Kill Devil Hills, NC (1%)
<i>P. relictus</i>	Auburn, NY/Presque Isle, PA (25%)
Rhynchiitidae	
<i>Eugnampius angustatus</i>	Lawrence, KS (12%)

cocoon, but the latter were not saved. Because multillids typically attack their host after it has formed a cocoon, with the multillid larva spinning its cocoon within the host cocoon (Mickel, 1928), we cannot decisively say that this *Cerceris* nest was not parasitized by the multillid. On the other hand, the only published host record for *Pseudomethoca sanbornii* is the halictid bee *Nomia pattoni* (Cockerell (= *Dieunomia nevadensis bakeri* Cockerell) (Mickel, 1924). Thus, if the mutillid has been correctly identified to species (which is by no means easy with female mutillids), its use of *Cerceris* and *Nomia* as hosts would represent an unusual host range. [*Dieunomia triangulifera* (Vachal) nested abundantly nearby.] On June 29, a mutillid (subsequently captured and identified as *Pseudomethoca simillima* Smith) entered a nest for 66 s. This nest was not excavated, and no host records have been published for *Pseudomethoca simillima*.

Some of the cells in the nests we excavated showed evidence of having fallen victim to cleptoparasites. Of 61 cells examined, 40 contained an immature

Cerceris (egg, larva, or cocoon), 2 contained practically intact prey but no immature *Cerceris* (although 1 of these cells had what appeared to be a desiccated wasp egg); 12 had remains of partially consumed prey but no larva, egg, or pupa of any kind, 5 contained decomposing prey in bad condition; 1 contained an ovoid cocoon distinctly different from that of *Cerceris*; and 1 cell was completely empty. The 12 cells with prey that had been partially consumed but no immature wasps were probably parasitized by miltogrammine larvae, which leave the cell after feeding and pupate in the soil. The ovoid cocoon found in a cell with prey remains was opened and found to contain a partially desiccated larva of an aculeate hymenopteran. Comparison with Evans' (1987) descriptions and illustrations of aculeate larvae suggests that this specimen could be a chrysidid and is probably not a mutillid (because the second thoracic spiracle is not greatly reduced in size).

If we have correctly identified cleptoparasitized cells, our estimate of the overall rate of parasitism in this population is somewhere between 13/61 (21%) and 17/61 (28%), depending on whether or not the five cells with partially decomposed prey are included in the tally of parasitized cells. However, three of the nests we excavated showed no signs of parasitism, two had some cells that may have been parasitized but were difficult to diagnose, and the other five nests had parasitism rates ranging from 12.5 to 50%.

It is possible that our practice of placing transparent plastic cups over the nest entrance may have influenced the susceptibility of these wasps to nest parasitism. Most of the parasites search for open nests, so they may have been deterred by the cups. To compensate partially for this effect, we would remove the cup when we saw a parasite searching in the vicinity of a nest, but miltogrammine flies are small and inconspicuous, so we may have failed to see them at times. Satellite flies in the genus *Senotainia*, which follow prey-laden wasps in flight and larviposit on the prey, may have benefited from the cups, because the wasps were forced to pause near the nest entrance (although we would remove the cup if we saw a wasp approaching a nest.) The only way to evaluate objectively the magnitude of the effect these cups may have on rates of nest parasitism would be to compare samples of cells from nests within and without cups placed over the entrance, and we do not have adequate sample sizes for a meaningful comparison. However, the rates of parasitism observed in our study lie within the range that other authors have reported for *Cerceris rufopicta*. In the two nests that Krombein (1952) excavated in North Carolina, parasitism rates were two of five cells (40%) and three of nine cells (33%). The one nest that Krombein (1964) excavated in Florida was not parasitized (one cell had a "moldy egg or young larva," but the beetle prey were described as "whole") and Evans (1971) made no mention of parasitism in the four nests from two sites that he studied in central New York. Kurczewski and Miller (1984) excavated two nests in New York and seven in Pennsylvania, and found one nest at

each site to be parasitized: one of two cells (50%) were parasitized in the New York nest, and two of three cells (67%) were parasitized in the Pennsylvania nest. The only general conclusion that can presently be drawn from these limited data is that rates of nest parasitism vary considerably within and among sites.

Patterns of Nest Occupancy

There are 19 nests for which we have records of occupancy for 2 or more days (Table IV). Four of these nests were occupied for only 2 days, in each case by only a single wasp. All but one of them were seen to be provisioned on one or both days that they were occupied.

Of the remaining 15 nests, 4 were occupied and provisioned by only a single individual during our study and were not entered by other wasps. Another three nests were only provisioned by a single individual, but other wasps were seen to enter the nest without prey. The other eight nests that were used for more than 2 days were definitely provisioned by more than one female, although there was only one case when two females provisioned the same nest on the same day.

A number of special circumstances are associated with the latter nest (Nest Z), which was provisioned by wasps GrS and BB on July 5. Although this nest had been marked on June 22, no activity had been recorded at the spot from June 23 to July 5. However, a mound of soil surrounding an open burrow was seen on the morning of July 5, so a plastic cup was placed over the nest. The first wasp seen at the nest was an unmarked female bringing in prey at 0951. She was captured and marked GrS when she emerged from the nest at 0953. At 1012 h, wasp BB (which had been marked on June 22), came to nest Z without prey, and closed the nest with a plug of soil after entering it. At 1036, GrS returned to the nest with prey, but found the entrance sealed and tried to dig through the closed entrance. In order to do this, she had to drop the prey she had been carrying, and during the three minutes that it took for her to enter the nest, the prey had walked away (albeit in a rather uncoordinated manner.) A few minutes later, GrS again left the nest, and in her absence the entrance was again sealed from inside. When she returned without prey at 1206, she briefly landed near the entrance, walked around for a few minutes, and then flew away. She was not seen again before the day's first observation period ended at 1400. During a second observation period later that day (from 1730 to 2100), wasp GrS was not seen, but wasp BB made two provisioning trips and a final nonprovisioning trip, after which she closed the nest from inside. The interactions between GrS and BB are very similar to those observed during other nest usurpations, but the uncertainty about when and by which wasp this nest was initiated and the fact that GrS was captured and marked on the morning

when she lost the nest she had been trying to provision make it unclear how this encounter should be interpreted.

A few nests, such as J, 6, and 2.6, were permanently abandoned early during the nesting season and never reoccupied, whereas other nests, such as 3 and 4, were abandoned for a few days and then used again by a different wasp (see Table IV). Because in these cases the cessation of provisioning by one wasp was not immediately associated with the onset of provisioning by another wasp, a likely explanation for the first wasp's disappearance is that she died during foraging, although other reasons (such as emigration from the study area) cannot be ruled out decisively.

We observed 21 cases in which a wasp tried to usurp a nest that was being provisioned by another wasp. These attempts were made while the owner of the nest was away. The usurper entered the open nest and closed the entrance from inside with a plug of soil, so that the owner found a sealed nest when she returned. Successful usurpation—i.e., change in ownership—took place on 7 of the 21 attempts; in the other cases, the owner expelled the usurper and then closed the nest from inside. Having succeeded in usurping a nest, a wasp would usually begin provisioning it within the next 2 days.

On three occasions, two wasps occupied the same nest, apparently throughout the night. However, in none of these cases did we observe the two wasps simultaneously provisioning the same nest. The wasps OGr and BR, who were provisioning nests F and H, respectively, were observed to place prey in other nests in spite of the fact that those nests were simultaneously occupied by other females who had been provisioning the nest for several days. These instances may have been due to the failure of the wasp to recognize her own nest, since the other nest into which she placed the prey was very close to the nest she had been provisioning. In any case, it is quite clear that on the following day each wasp resumed provisioning the same nest she had previously been provisioning.

A wasp who was expelled from her nest by a usurper would usually make an effort to get it back, although when such efforts failed she would not persist for long, but would instead start searching for another nest. Three wasps whose nest had been usurped were able to usurp another nest within 1 or 2 days, and another usurped female occupied a nest that had been abandoned.

Thirteen of the twenty-one attempts at usurpation, including six of the seven that were successful, took place between July 4 and July 7, following a major change in the nesting area. An unknown number of nests had been eliminated or altered as a consequence of harvesting, plowing, and replanting of cultivated field adjacent to the area where we were monitoring nests. Portions of the dirt road in which the wasps had been nesting were temporarily destroyed by plowing (although the farmers did not disturb the area we were monitoring), and the road was reinstated after the field was replanted.

Table IV. Daily Records of Nest Occupancy and Provisioning Activity at Monitored Nests. Dates are Designated as Month/Day, as in Table I. As Explained in the Text, Observations were Cancelled on June 25, 26, and 28 and on July 9-12. The Row Labelled “# Hours” Shows the Total Number of Hours that a Group of Nests was Observed on a Given Day. Entries in the Row Corresponding to Each Nest Show the Wasp(s) (Designated by Symbols such as WW, GoGo; a ? Designates an Unmarked Individual) that was/were Seen Entering that Nest on a Given Day (Underlined Boldface Type Indicates a Change in Occupancy.) The Number Below the Symbol for a Given Wasp on a Given Day Shows How Many Provisioning Trips that Wasp Made; a Value of 0 Indicates that the Wasp Made One or More Trips Away from the Nest, but was not Seen to Bring in Prey on that Day; an Entry of n.a. Means that No Wasp was Seen to Enter or Leave the Nest on that Day; No entry at All on a Given Date Means that the Nest was not Yet Being Monitored. Nests on this Page (None of which were Active on July 16 or 17) were Monitored by BAA, Those on the Facing Page were Monitored by JDA.

Nest	Date															
	06/23	06/24	06/27	06/29	06/30	07/01	07/02	07/03	07/04	07/05	07/06	07/07	07/08	07/13	07/14	07/15
Number of hours	6	3	3	6	6	7	6	3.5	4	8	3	3	3	6	5.5	4
C	WW	WW	WW	WW	WW	WW	WW	WW	WW	WW	WW	n.a.	WW	?	B/B	B/B
J	1 GoGo	1 GoGo	0? n.a.	5 n.a.	6 n.a.	7 n.a.	1 n.a.	3 n.a.	4 n.a.	4 n.a.	3 n.a.	n.a.	2 n.a.	0 n.a.	2? n.a.	1? n.a.
3	1 GoR	0? GoR	1 GoR	1 GoR	n.a.	n.a.	n.a.	n.a.	<u>OB</u>	<u>BGo</u>	BGo	BGo	BGo	n.a.	n.a.	n.a.
H	17 BR	7 RGr	1 BR	1 BR	BR	BR	BR	OR	1? BR(4)	1 BR	3+1? BR	2 n.a.	3+2? BR	n.a.	n.a.	n.a.
4	5+1? BGo	0 BGo	3 BGo	8 BGo	5 BGo	2 BGo	3 BGo	0 BGo	OO(0) n.a.	4+1? n.a.	2 -O	2 WR	5 WR	n.a.	n.a.	n.a.
Z	5+1? 0?	0?	1	8	3	2+1?	0	0	n.a.	n.a.	5	0	2	n.a.	n.a.	n.a.
								<u>BR(3)</u>		GrS(1) BB(2) RB 0	BB 2 n.a.	n.a.	BB 1 O 2+1?	n.a.	n.a.	n.a.
3.5												GrS	GrS	n.a.	B-(0) ?(0)	?
7.7														n.a.	n.a.	(0) n.a.

DISCUSSION

As documented in the previous section, most aspects of nest architecture and prey choice in our study population lie within the range of variation reported for eastern populations of *Cerceris rufopicta*. Thus, the behavioral data are consistent with Ferguson's (1983) judgment that patterns of morphological variation indicate that *Cerceris rufopicta* is a single species whose range extends from the east coast to the central states of the United States. New prey records reported in this study represent a minority of provisioning bouts late in the nesting season and may reflect choices necessitated by the unavailability of preferred prey. In any case, the wasp who provisioned her last two cells with rhynchitid weevils and miscellaneous small chrysomelids had previously been using the same two prey species used by the other wasps in the population.

Evans and Rubink (1978) noted that "prey constancy," which they defined as the tendency of a species throughout its range "to utilize beetles of only one family, often of only a few related genera," is a striking characteristic of the behavior of *Cerceris* (although they also called attention to an apparent exception to this general rule). Gess (1980) provided a list of prey of 13 species of *Cerceris*, showing that for some species "prey constancy" could be broadened to involve utilization of species of a single order, in this case Hymenoptera rather than beetles. Grandi (1961) reported *C. rubida* gathering beetles for five families. Is this prey constancy on Coleoptera or prey inconsistency? Our data on *Cerceris rufopicta* conform to Evans and Rubink's general rule. The one striking exception that we observed hints that occasional exceptions to the general rule may occur toward the end of the normal nesting period, perhaps because preferred prey became scarce. Other authors, such as Bridwell (cited by Scullen 1965), have also suggested that unavailability of the usual preferred prey may force *Cerceris* wasps to utilize unusual prey occasionally. At the same time, we consider the anomalous prey records to be as noteworthy as the prey constancy exhibited in most circumstances, because such anomalies demonstrate that the wasps can be more flexible than they ordinarily are. Designing experiments to test the effects of prey availability on wasp selectivity would be logistically challenging, but the results would be of considerable interest.

Both the dimensions of individual cells and the total biomass of prey stored in each cell were slightly greater in our population than in the populations in New York and Pennsylvania studied by Kurczewski and Miller (1984). The mean wet weight of prey captured by the Kansas wasps was also somewhat greater, although the number of prey per cell was similar. Various authors have reported the existence of two types of cells in several species of *Cerceris*, one with a large amount of prey, which would be appropriate for rearing a female wasp, the other with fewer and/or smaller prey, appropriate for rearing a male wasp (Linsley and MacSwain, 1956; Evans, 1971; Alcock, 1974; Evans and

Rubink, 1978; Kurczewski and Miller, 1984). Although the data from our study and that of Kurczewski and Miller are limited, they do not seem to indicate a strong bimodality in cell types in the nests of *Cerceris rufopicta*. Depending on how one chooses to define the intervals along the axis representing number of prey per cell, one can draw a frequency histogram that looks distinctly unimodal or weakly bimodal, but in the latter case the two "modes" are at six prey/cell and eight prey/cell. Given the overall range in number of prey per cell that we found (3 to 22; mean = 7.75), the difference between these two "modes" seems unlikely to represent two distinct subgroups corresponding to male- and female-destined larvae. There are also other species of *Cerceris* that lack a striking bimodality in cell types (Kurczewski and Miller, 1984; Asis *et al.*, 1997), so more information on geographic and phylogenetic patterns of variation in this aspect of provisioning behavior is needed.

Despite the overall similarities in the nesting biology of eastern and western populations of *Cerceris rufopicta*, some noteworthy differences also seem to exist. Krombein (1952, 1953) reported that the females he studied in North Carolina often closed the nest after bringing in prey. Such behavior was very rare in the population we studied in Kansas—we observed it in only 11 of 355 provisioning trips (3%). One of the most striking things that we observed in this study was the prolonged period of time during which provisioning activity took place within the aggregation as a whole each day. This differed not only from what Krombein (1952, 1953) reported for North Carolina populations of *Cerceris rufopicta*, but also from what many other authors have reported for other temperate zone species of *Cerceris*. Linsley and MacSwain (1956), Alcock (1974), Byers (1978), Mueller *et al.* (1992), and Asis *et al.* (1997) have noted daily activity periods of 6 to 9 h, whereas the daily activity period often lasted for more than 12 h in our study population. No individual wasp was active for that many hours, so the distinctive feature of the Kansas population seems to be less synchrony in activity periods of different individuals within the aggregation.

Our study provides considerably more detail than as previously been available concerning individual variation in patterns of provisioning and nest occupancy in *Cerceris rufopicta*. However, we consider our results far from definitive. In fact, we feel more like we have opened a Pandora's box that reveals the superficiality of our current understanding of this species. We have observed that some individuals consistently occupy and provision a single nest throughout their adult lives, whereas others occupy a series of nests, sometimes by usurping them from other wasps. However, we know very little about the factors responsible for these differences, or how the behavioral differences affect the lifetime reproductive success of the wasps. Much of the nest usurpation that we observed was correlated with human disturbances that probably drove many wasps from their nests. Is this level of disturbance a relatively new factor in the evolutionary

history of this species, or is it approximately equivalent to disruptions of wasp nesting activities caused by "natural" agents prior to the time when humans became the predominant force shaping the landscape? Are the intensity and frequency of large-scale disruptions of nesting activities significant factors influencing the costs and benefits of behaviors such as nest usurpation and nest sharing? We were amazed to see a few wasps continuing to provision nests that had been hidden among dense stalks of wheat one evening and were at the edge of a vast expanse of bare earth the next morning.⁴ However, this area has been under cultivation for many wasp generations, so wasps that cannot tolerate the disruptions of their nesting area caused by farmers would presumably have been driven away long ago. Furthermore, *C. rufopicta* is a species whose native range seems to coincide fairly closely with the distribution of temperate deciduous forest at the time North America was originally settled by Europeans. Despite this apparent association with forested regions, *C. rufopicta* consistently nests in areas of firmly compacted soil with sparse vegetation, and in a forested region such habitats are likely to be associated with some kind of periodic disturbance. If *C. rufopicta* is a species that preferentially nests in disturbed habitats, perhaps we should not be surprised at evidence of considerable plasticity in its patterns of nest occupancy.

Researchers interested in the early stages of the evolution of social behavior have devoted a great deal of attention to measuring the costs and benefits of various behavioral options of members of social groups. However, far less attention has been paid to behavioral variation and its consequences in solitary species of wasps and bees. There is little question that solitary nest provisioning was the starting point for the evolution of social behavior in wasps and bees, and the more we learn about the lives of these solitary species, the more complex we find them to be. Noteworthy examples of variation in patterns of nesting behavior in solitary apoid wasps are documented in the studies by Brockmann and colleagues on *Sphex ichneumoneus* (Brockmann and Dawkins, 1979; Brockmann *et al.*, 1979) and *Trypoxylon politum* (Brockmann, 1980) and by Field on *Ammophila sabulosa* (Field, 1989a, b) and *Cerceris arenaria* (Field, 1995). In order to understand truly how some wasps and bees came to live in social groups, we must develop a much deeper understanding than we currently have about the circumstances in which their close relatives remain solitary.

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⁴These nests were not in the area we regularly monitored, but we had marked them at the start of our study.

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