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2. Effects of prey size and load carriage on the evolution of foraging strategies in wasps

Joseph R. Coelho
Institute for Franciscan Environmental Studies, Biology Program, Quincy University
1800 College Ave, Quincy, IL 62301, USA

Abstract. Load-carriage limits should impose constraints on foraging for wasps that carry prey in flight. However, application of a simple foraging model to a variety of such wasps reveals a diversity of evolved solutions to the problems of load carriage, as well as often greater constraints imposed by the environment. Some wasps are able to carry loads greater than that with which they should be able to take off. Some wasps are limited in prey size optimization by the availability of prey sizes, others by prey stealing behavior of conspecifics or by the location of their nests. Even species which appear to be nearly perfect in utilizing their foraging capacity may demonstrate low precision upon closer inspection. The ability of wasps to assess prey size and to switch prey species should be explored further. Studies of foraging behavior in the field, rather than at the nest site, might provide greater insight into wasps' abilities to optimize loading.

Introduction

Wasp foraging behavior has been the subject of several classic natural history studies [1, 2, 3, 4], as it is fascinating to observe. It is only recently,

Correspondence/Reprint request: Dr. Joseph R. Coelho, Institute for Franciscan Environmental Studies Biology Program, Quincy University, 1800 College Ave, Quincy, IL 62301, USA. E-mail: coelhjo@quincy.edu

however, that formalized quantitative efforts have been applied to wasp foraging [e.g. 5, 6]. In this regard, wasps have proven excellent models, yielding interesting insights into the evolution of foraging behavior. Being relatively small, abundant and, frequently, returning to the same site (nest) repeatedly has made wasps convenient study organisms. If energy supplies are limited, selection should favor individuals most effective at acquiring energy [7]. One model of foraging efficiency (modified from [8]) is as follows:

$$E/T=(N_eE-C_s)/(1+N_eH)$$

where

N_e=prey encounter rate
E=energy gain/prey
C_s=cost of searching
H=handling time
T=time

Hence, selection should favor predators that maximize E/T. All other things being equal, larger prey yields larger E return. Hence, a predator should maximize E by taking the largest prey items available (although increasing load size may also increase the energy cost of flying [9] and decrease foraging lifespan [10]). This principle should be particularly applicable to predaceous wasps, as most are specialized predators of restricted taxa, and all prey of a given taxon are likely to have a similar energetic value. Thus, E does not vary so much with prey type as prey size. For many predatory wasps, prey size maxima may be limited by the physical constraints of flying with the prey.

One method used to examining foraging decisions in wasps is to predict the optimal load size of the prey, and to compare this prediction to the size of actual prey loads. Fortunately, the optimal load size is simple to calculate for species that carry the prey in flight, as the force production of flying animals is primarily dependent on their flight muscle mass. The maximum force produced must equal the weight of the wasp plus that of the prey if the wasp is to fly. At the maximum load mass, the ratio of flight muscle mass to body plus prey mass (or flight muscle ratio) is 0.179 for Hymenoptera [11]. In other words, if the wasp has a prey item so large that flight muscle ratio < 0.179, it cannot take off, and the foraging bout fails. Use of this threshold, the marginal flight muscle ratio, as a metric for flight capability has several advantages, primarily its independence of the size of the wasp, allowing it to be used in cross-species comparisons.

This simple model and methodology have been applied to several species of wasps not so much as a formal test of foraging theory but as a means of examining behavioral alternatives that have evolved in each species. The ecological context of each species imposes limitations and opportunities that affect its behavior.

Methods

In each study essentially the same techniques were used. Wasps carrying prey were captured, usually as they returned to the nest. The body masses of the wasp and prey were measured fresh or frozen (never dried). The thorax mass of the wasp was determined by cutting away legs, wings, head and abdomen and weighing the remaining thorax on a balance. As flight muscle comprises 95% of the thorax in Hymenoptera [11], the flight muscle need not be dissected out and weighed separately.

Discussion

Yellowjackets (*Vespula*) are social wasps that prey upon or scavenge a variety of foodstuffs. Normally, undertaker honey bees (*Apis mellifera* L.), carry their dead far from the hive [12]. However, when the thorax temperatures of honeybees are measured (by stabbing with a thermocouple probe, e.g. [13]), discarded dead bees rapidly accumulate near the hive. The investigator noticed opportunistic yellowjackets consuming them with considerable zeal. When foraging on dead honey bees, yellowjackets chew body parts off the carcass until they are able to take off with the remaining portion of it. The first parts chewed away are generally not very nutritious—legs and wings. Still, one would predict that a yellowjacket should chew away just enough material to reduce its FMR_o to 0.179, thereby maximizing the caloric intake of the colony. This hypothesis was tested in three species of *Vespula* [5]. In neither case did a wasp species achieve the ideal FMR_o (Table 1). The nearest to approach the optimal loading was the largest, the German yellowjacket (*V. germanica* [Fab.]), at FMR_o=0.220. *V. squamosa* (Drury) achieved only 0.289, while the smallest, *V. maculifrons* (Buysson), declined to forage on dead honeybees at all.

The reason for the apparent suboptimality of the first two species appears to lie in the technique used to dismember the honey bee corpse. *V. germanica*, being the largest species, was occasionally able to carry an entire bee corpse; however, when it was unable to do so, it chewed through the narrowest portions of the body—the petiole and cervix. Hence, discrete tagmata of the bee corpse were taken. Such a body segment, while carryable,

Table 1. Average body mass (M_b) of wasps and prey, and resulting flight muscle ratios of wasps while unladen (FMR) and laden with prey (FMR_o). All prey are paralyzed adults unless otherwise noted. The marginal flight muscle ratio, the minimum at which the wasp can just take off, is 0.179 (11).

Wasp species	**Wasp M_b (g)**	**Prey type**	**Prey M_b (g)**	**FMR**	**FMR_o**	**Reference**
Bembix troglodytes	0.099	Diptera	0.045	0.358	0.285	[26]
Monobia quadridens	0.218	Pyralidae (larvae)	0.108	0.385	0.263	[22]
Sceliphron caementarium	0.129	Aranea	0.034	0.423	0.364	[14]
Sceliphron spirifex	0.132	Aranea	0.077	0.409	0.258	[24]
Sphecius convallis	0.991	*Tibicen parallelus*	1.127	0.401	0.187	[14]
Sphecius speciosus	0.822	*Tibicen* spp.	1.541	0.433	0.142	[16]
Sphecius speciosus	0.557	*Neocicada hieroglyphica*	0.298	0.380	0.248	[14]
Sphex ichneumoneus	0.303	Conocephalinae	0.331	0.462	0.238	[20]
Sphex pennsylvanicus	0.489	Phaneropterinae	0.697	0.425	0.189	[14]
Stizus continuus	0.184	Acrididae	0.188	0.380	0.200	[6]
Tachytes chrysopyga	0.052	Orthoptera	0.050	0.334	0.177	[26]
Vespula germanica	0.092	*Apis mellifera* (dead)	0.045	0.330	0.220	[5]
Vespula squamosa	0.056	*Apis mellifera* (dead)	0.022	0.400	0.289	[5]

might not meet the maximum load. To do so perfectly (to maximize E) would require chewing through the full thickness of the thorax or abdomen. The lengthy H accrued by such a task would reduce foraging efficiency. *V. maculifrons* would not forage on honey bee corpses in spite of a variety of efforts to induce them to do so. Calculations indicate that they would have difficulty carrying a bee thorax. While carrying a head was possible, the low nutritional value might not be worth their time.

Larger wasps carried larger loads within species and among species, indicating some degree the wasps' ability to maximize *E* through prey size. Interestingly, *V. germanica* foraging on honey bees were 36% larger than a sample collected at a nest. Similarly, foraging *V. squamosa* were 10% larger by body mass, suggesting the possibility of polyethism, or that workers may specialize on foods that are suitable to their body size. The largest *V. germanica*, which were sometimes able to carry entire bee carcasses, both optimized the prey size and minimized handling time.

The ability to macerate prey probably contributes greatly to the broad generalist foraging capabilities of social yellowjackets. By contrast, all the species discussed below are not only solitary, they forage on a narrow group of taxa. They carry their prey intact, and never chew off parts of it. The first of these species to be examined was the eastern cicada killer (*Sphecius speciosus* Drury). Cicada killer females, as their name implies, forage exclusively on cicadas (Hemiptera: Cicadidae). Finding their prey usually in a tree, they sting it. Complete, permanent paralysis results in less than 60 s [14]. The wasp grasps the cicada ventral side up and flies to its burrow, where it sequesters it in a cell and lays an egg on it, or obtains another cicada [15]. The implausible sight of a female cicada killer, itself nearly one gram in body mass, attempting to carry a cicada even larger than itself, immediately raises questions of load carriage and difficulty in flight.

Figure 1. *Sphecius speciosus* using midlegs to drag *Tibicen* spp. overland in the vicinity of the burrow. Will County, IL, USA (photo by Joe Coelho).

At sites in Indiana and Illinois (USA) eastern cicada killers foraged on species of *Tibicen*, reducing their FMR_0 to levels well below those with which they should have been able to carry the cicada [16]. These populations of cicada killers had the lowest mean FMR_0 of all wasps examined. Only 10% of cicada killers should have been able to take off with their prey. However, cicada killers are prodigious foragers, securing between seven and eight cicadas per day on average [17]. Part of the reason for the foraging success of cicada killers lies in the plasticity of their load carriage behavior: they can climb trees while carrying prey. Once the wasp has flown as far as it can with the cicada, presumably downward even under maximum power, it crawls about and finds a vertical object. It ascends the object, usually a tree, until it reaches a height, and takes off again. By repeating this sequence, the wasp eventually gains its burrow. Often the wasp reaches the burrow in flight, but occasionally the wasp is seen hauling the prey overland. This process, as well as climbing, is facilitated by the wasp clasping the cicada with the middle pair of legs, leaving the forelegs and hindlegs for walking. The careful observer will see that the pretarsi of the midleg closely fit a ridge at the base of the cicada's wing, providing a firm grip while also holding the wings of the cicada closed. Any vertical object will serve for climbing purposes, including humans willing to hold still. On one occasion a female cicada killer with prey was observed climbing a vertical pipe to its top, approximately 2 m, and flying to the ground. However, her wings were so thoroughly worn that she could not generate much horizontal displacement. In searching for another vertical object, she climbed the same pipe again and again. Eventually, she dropped the cicada, and it was taken by another female [14].

Prey carriage is often difficult for eastern cicada killers. Paralyzed cicadas are dropped from trees for reasons unknown or left on the ground when obstacles between wasp and burrow are seemingly insurmountable (e.g. dense, high grass). These prey are usually abandoned, and devoured by scavengers such as ants and yellowjackets. In cicada killers, long powerful legs, climbing ability, and abundant prey allow them to be even more efficient foragers than predicted.

Behavioral plasticity in foraging behavior also appears to contribute to the success of cicada killers. Again, dropped cicadas are usually abandoned, except apparently at large, high-density nesting sites (described in [18]), where other females will pick them up (as described above). Prey stealing may also occur at such high densities. While such behaviors might appear to improve foraging by shortening the distance traveled and time spent returning with prey, there must be disadvantages as well. At numerous other sites observed by these investigators over a large geographical area, these behaviors were rarely observed. Probably, the frequency of cicadas dropped or available for theft is much lower at sites of average or lower density. Recently, an unusual population of cicada killers was discovered in Florida (USA), in which the primary prey species, *Neocicada hieroglyphica* (Say), is rather small [19]. The female eastern cicada killer is also reduced in size, but not as much. As a result, the wasp enjoys a much higher FMR_o (0.25) than populations using the much larger *Tibicen*. None of the females in the sample (n=14) had $FMR_o < 0.179$, and none was observed climbing with prey to achieve altitude [14]. Loading is less than ideal, and females provision each cell with more cicadas to compensate for small prey size. Hence, variation in prey species availability can affect the foraging behavior and efficiency at the population level.

The great golden digger wasp (*Sphex ichneumoneus* L.) also digs a burrow, but forages on orthopteran prey. Although somewhat smaller in body size than *Sphecius*, it has the highest FMR of any wasp, at 0.46 [20]. This mass allocation is favorable to foraging on quite large prey, which are primarily tettigoniids. When thus burdened, the FMR_o of *S. ichneumoneus* is reduced to 0.238 on average. However, 25% of wasps had $FMR_o < 0.179$, indicating that *Sphex ichneumoneus* is frequently overloaded (Fig. 2).

The great golden digger wasp arrives at essentially the same solution to this problem as *Sphecius*: climbing. The prey of *Sphex ichneumoneus*, however,

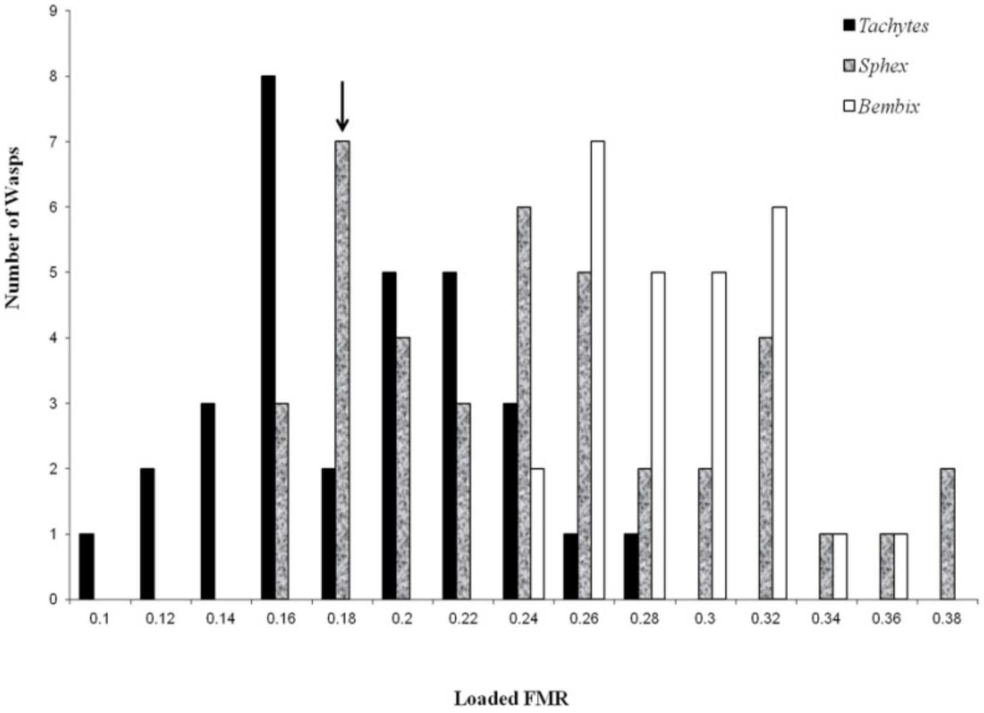

Figure 2. The distribution of operational flight muscle ratios in three solitary wasps (*Tachytes* and *Bembix* from [25], *Sphex* from [20]). The arrow indicates the marginal flight muscle ratio, where take-off is just possible [11].

is normally found in low vegetation, making more frequent climb-and-fly cycles necessary. When climbing is not an option, *Sphex ichneumoneus* beats its wings while dragging its prey overland. Prey that are too large to be carried are abandoned [21]. As the nesting season progresses and prey species grow larger, *Sphex ichneumoneus* may switch to smaller prey [21]. However, no change in FMR_0 occurs over time [20]. Prey size and wasp size are correlated. Various lines of evidence suggest the ability of *S. ichneumoneus* to learn to assess prey size during foraging, and adjust choice of prey size (see discussion in [19]). This phenomenon should be studied further to determine its pervasiveness and capacity to improve foraging efficiency in solitary wasps.

Sphex pennsylvanicus L., the great black digger wasp, was found foraging on various katydids (Orthoptera: Phaneropterinae), including *Amblycorypha, Microcentrum,* and *Scudderia* (Fig. 3). Females flew in with prey, landing very close to their destination, a crack in a concrete porch, beyond which individual burrows presumably lay. Prey were frequently dropped, and

Figure 3. *Sphex pennsylvanicus* with katydid prey. Lewis County, MO, USA (photo by Joe Coelho).

prey theft was common. In spite of being 61% larger than its aforementioned congener, *Sphex pennsylvanicus* had 8% lower FMR. Moreover, the prey were 110% larger, contributing to a 24% lower FMR_o [14]. Although the FMR_o was near optimal, the range was quite broad (0.131-0.230) and the sample size low (n=9). Some females (4 of 9) were apparently overloaded. Though climbing was not observed, it could have occurred in large nearby trees.

The carpenter wasp (*Monobia quadridens* L.) is an aerial-nesting eumenid, using primarily vacant carpenter bee (*Xylocopa*) borings for nests [22]. It also readily uses wooden trap nests with 1-cm diameter holes. The carpenter wasp mass provisions a cell with paralyzed lepidopteran caterpillars [22], lays an egg, seals the cell with mud, and begins provisioning the next cell in the series. In west-central Illinois (USA), prey are mostly pyralid moths. As an aerial nester, the carpenter wasp cannot easily use the same tricks as *Sphecius* and *Sphex* (climbing) to carry oversized prey, at least not for the final approach to to its nest. Not surprisingly, the mean FMR_o of carpenter wasps carrying caterpillars was 0.263, well above the marginal FMR. The size of caterpillars taken, however, increased linearly over time, approximately doubling during the May to September active season, resulting in a corresponding linear decline in FMR_o. These trends result in caterpillars that are too light early in the season and too heavy later in the season. Behavioral flexibility allows the carpenter wasp to compensate in part for this apparent environmental constraint. When caterpillars are small, the wasp may carry two at one time. When caterpillars are large, FMR_o may fall below the marginal level (5.6% of all cases). Some wasps attempt to drag the oversized caterpillars up the woodwork to the nest. These efforts often fail, however, and the prey is dropped and abandoned [22]. Seasonal growth of prey occurs in other wasps [21, 23], and some switch prey species to compensate [21]. Perhaps small caterpillars are simply unavailable at the end of summer, disallowing prey switching. In the case of the carpenter wasp, the nesting habit and environmental effects appear to constrain foraging capacity.

Mud daubers of the genus *Sceliphron* (Crabronidae) also are aerial nesters, but form their nests almost entirely from mud, and mass provision their larvae with spiders (Fig. 4). Two species, *Sceliphron spirifex* L. and *Sceliphron caementarium* (Drury) have been examined [14, 24]. Though native to different continents, the two mud daubers are remarkably similar in size and FMR. In both cases, FMR_o was well above the marginal level, and no individual carried a spider that brought FMR_o below the marginal level. Unfortunately, sample sizes are small in both cases (n=4 for *Sceliphron spirifex*). For *Sceliphron caementarium* (n=29), the black and yellow mud dauber, a 12x range of prey M_b was observed, but even the largest spider

Figure 4. *Sceliphron caementarium,* the black and yellow mud dauber, carries spider prey with its mandibles. Its nests are constructed in a sheltered area, in this case, a garden shed. Lewis County, MO, USA (photo by Joe Coelho).

(M_b=0.127g) depressed FMR_o only to 0.25. *Sceliphron caementarium* has the highest mean FMR_o of wasps examined. Hence, it appears tentatively that aerial nesting limits mud daubers to prey items below the maximal load-lifting capacity at take-off. However, growth of spider prey may make it more difficult for them to carry late in the season [23]. Hence, this genus should be examined more thoroughly, especially at different times of the nesting season, to determine whether the pattern of light loads holds.

Bembix troglodytes Handlirsch is a ground-nesting, progressively provisioning crabronid wasp that forages on flies (Diptera). *Bembix* is adept at exploiting the most abundant flies by learning sites with high densities of flies and visiting them repeatedly [25]. This behavioral flexibility suggested that *B. troglodytes* might be able to select flies of ideal size to optimize load carriage on the return trip to the nest [26]. On the contrary, foraging females reduced their FMR (0.36) to an FMR_o of only 0.29 at a site in Big Bend National Park (Texas, USA), resulting in the second highest average FMR_o among species examined herein. In fact, no foraging female had FMR_o equal to or lower than the marginal level (Fig. 2). The possible reasons for lack of optimization were readily apparent to the observers. Nearly every female returning to a burrow with prey was immediately pounced upon by conspecific females. Prey were often dropped during the attack, then stolen by another female. Many aspects of the females' foraging behavior seemed to be adapted to minimizing prey theft. The fly was tucked tightly under the body of the wasp and held with all legs, making it difficult to determine whether the female was carrying prey at all. The high FMR_o of prey-laden females made them quite maneuverable and difficult to capture. In a related wasp (*Stictia heros* [Fabr.]), the prey size is directly related to the probability of attempted prey theft [27]. Abundant brood parasites, such as velvet ants and satellite flies, also made speed in securing the prey in the burrow advantageous. Therefore, being an apparently suboptimal forager relative to prey size may actually optimize foraging by discouraging prey theft and brood parasitism, while attempted prey stealing was rarely observed in the other species treated in this review.

Tachytes chrysopyga obscurus Cresson is a small (the smallest discussed herein) solitary wasp that mass provisions its earth burrows with various orthopteran prey (Fig. 5). It packs each cell of its complex burrow with up to 10 prey items before laying an egg within [28]. *Tachytes chrysopyga* in Will County, Illinois (USA), were found in a large colony within an even larger colony of eastern cicada killers [25]. *Tachytes chrysopyga* females' FMR was a modest 0.33. However, when laden with prey, the FMR_o of such females averaged 0.18, almost exactly the marginal level. Could *T. chrysopyga* be a true optimal forager? Inspection of the distribution of FMR_o reveals otherwise

Figure 5. *Tachytes chrysopyga* carrying grasshopper prey over the substrate, occasionally making short, hopping flights. Will County, IL, USA (photo by Joe Coelho).

(Fig. 2). Although the marginal FMR_o falls within the 95% confidence interval of the mean FMR_o, the range of FMR_o is very broad. Wasp behavior matched the variation in FMR_o. Some prey-laden females were fast and manueverable on the wing, while others used short, hopping flights to return to the burrow. While weak stabilizing selection may be acting on prey size selection in *T. chrysopyga,* its behavioral plasticity allows it to forage on a ten-fold range of prey masses. Like many of the wasps described herein, *T. chrysopyga* is probably opportunistic, attempting to forage on the first suitable prey it encounters rather than wasting time and energy looking for prey of ideal size.

Nearly ideal loading was observed in another ground-nesting, solitary, orthopteran-hunting wasp, *Stizus continuus* (Klug). Loaded females (Fig. 6) had mean FMR_o of 0.20 [6]. Fifteen individuals (38%) were overloaded, having $FMR_o < 0.179$. With a standard error of 0.05 (n=39), variation was also considerable. The similarity to *Tachytes* ends there, as *Stizus continuus* is 3.5x the body mass of *Tachytes chrysopyga*. The authors suggest that overloaded wasps may climb objects in the environment to gain height. Prey species selection is nonrandom in *Stizus continuus*, and appears to be related to preferred hunting habitat [6], large bushes, from which wasps could descend with large prey, which was observed, though infrequently [Polidori, pers. comm.].

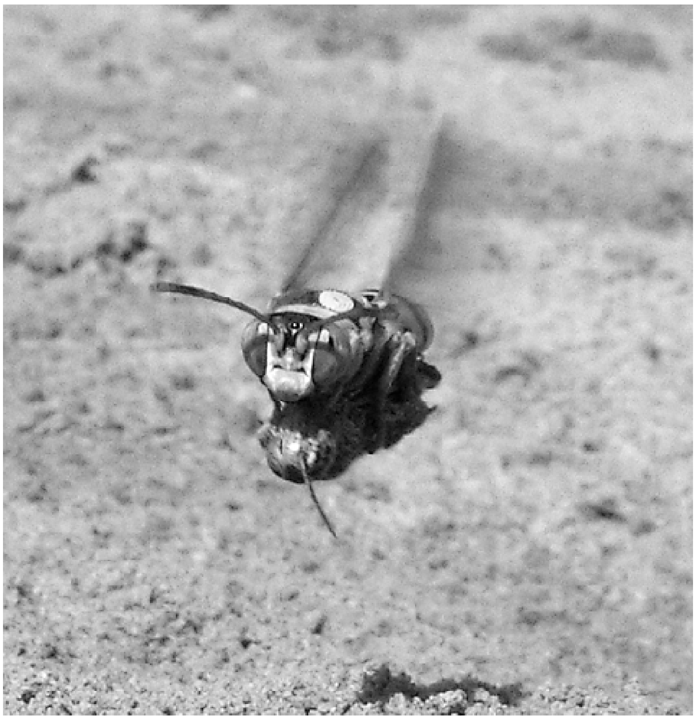

Figure 6. *Stizus continuus* carrying prey in flight. El Saler, Valencia, Spain (photo by Davide Santoro).

Recently, the Pacific cicada killer, *Sphecius convallis* Patton (Fig. 7), was studied in Ruby (Santa Cruz County), Arizona [14]. This population preyed exclusively on *Tibicen parallelus* Davis, resulting in a mean FMR_o of 0.187 (n=46). This value lies just above the marginal level, and only seven wasps (15%) were below 0.179. The low standard error (0.002) suggests that *S. convallis* is the most ideal flying predatory wasp so far examined with respect to loading. The fact that this population preys on adults of a single cicada species may allow stabilizing selection to adjust the size of adult females to a nearly optimal level.

Figure 7. *Sphecius convallis* carrying *Tibicen parallelus* in flight casts a shadow on sandy mine tailings where it nests. Santa Cruz Co., AZ, USA (photo by Joe Coelho).

Conclusions

Studies of load carriage have provided interesting insights into the foraging behavior of wasps. It appears that few wasps are “optimal” foragers in the sense that they achieve the ideal FMR_o of 0.179 during foraging. In most cases, the biotic environment imposes limits or conditions which prevent optimality from being achieved. Wasps appear to have evolved toward optimal load carriage, but usually without achieving it because of the particular constraints to which each is subjected. There is an incredibly diverse array of behaviors exhibited by wasps to circumvent limitations imposed by load-lifting, prey diversity, prey developmental stage, prey theft and other environmental stressors. It cannot be doubted that continued examination of wasp foraging behavior in this manner will reveal additional, unexpected behavioral adaptations.

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