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Aerial Prey Caching by Solitary Ground-Nesting Wasps: A Test of the Predator Defense Hypothesis

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Many solitary ground-nesting wasps in the families Pompilidae and Sphecidae excavate nests after capturing prey for provisions. These wasps generally cache their immobilized prey temporarily during nest excavation, frequently by suspending the prey in a plant (''aerial caching''). Here I test the hypothesis that aerial caching by Ammophila spp. wasps (Sphecidae) functions to reduce prey theft by generalist predators, Formica spp. ants. Foraging ants removed baits placed on the ground more rapidly than baits suspended in plants; mean half-lives for ground and aerial baits were 14.5 and 145.7 min, respectively (mean values for experiments 1-3). Ant foraging activity decreased during the midday. Ant interference with nesting activities of Ammophila spp. also decreased during the midday, paralleling observed fluctuations in ant foraging activity.

KEY WORDS: antipredator behavior; prey caching; *Ammophila*; *Formica*; foraging behavior; Hymenoptera.

INTRODUCTION

The entomophagous Hymenoptera exhibit a diversity of behavior patterns, ranging from primitive parasitoid habits to those of the highly derived eusocial nest-builders. Two early evolutionary modifications of parasitoid behavior yielded behavior patterns that included, first, the movement of the paralyzed host into a preexisting place of concealment, or ''niche,'' before depositing an egg (a prey-niche-egg sequence) and, second, the construction of a nest to house the host and developing offspring (a prey-nest-egg sequence) (Evans, 1958).

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Prey-nest-egg sequences are found in many genera of the Pompilidae and in four genera of the sphecid subfamily Sphecinae, *Palmodes*, *Prionyx*, *Podalonia*, and *Ammophila* (Iwata, 1976). During nest excavation these wasps only rarely leave the immobilized prey exposed on the soil surface (e.g., Evans, 1958); rather, prey are temporarily cached, most frequently by being suspended in a plant (''aerial caching'') and less commonly by being placed on the ground beneath plants or in a preexisting crevice or burrow (Evans, 1958, 1966, 1970, 1987; Iwata, 1976; O'Brien and Kurczewski, 1982; O'Brien, 1983; Alm and Kurczewski, 1984; Weaving, 1984).

Aerial prey caching has been hypothesized to function as (i) a defense against prey theft by surface-foraging predatory insects, including ants and carabid and cicindellid beetles (Newcomer, 1930; Evans, 1966; Malyshev, 1968; O'Brien and Kurczewski, 1982), (ii) a defense against cleptoparasites (Malyshev, 1968), and (iii) a means of minimizing prey dessication (O'Brien and Kurczewski, 1982). Although limited anecdotal evidence supporting an antipredator function has been reported (e.g., O'Brien and Kurczewski, 1982), none of these hypotheses has been tested experimentally.

Here I report experimental tests of the hypothesis that aerial prey caching decreases the likelihood of prey theft by ants, primarily *Formica sibylla* W. M. Wheeler (Hymenoptera: Formicidae), in nesting areas of the solitary ground-nesting wasp *Ammophila marshi* Menke (Hymenoptera: Sphecidae). Within-day variation in ant foraging activity and resulting variation in the risk of prey theft and other forms of ant interference with *A. marshi*, *Ammophila dysmica*, Menke, and *Ammophila azteca* Cameron are also reported.

MATERIALS AND METHODS

The study was conducted 1983–1988 at the University of California's Sagehen Creek Field Station, Nevada County, in the Sierra Nevada Mountains. The 0.125-km^2 study site, elevation 2000 m, had been deforested by a 1960 fire, and was dominated by the shrubby *Ceanothus velutinus* Dougl. ex Hook. Nesting activity occurred in open areas in mixed-species aggregations (mainly *A. dysmica* and *A. azteca*) and in relative isolation (mainly *A. marshi*). *Ammophila* spp. excavate shallow unicellular nests and provision with lepidopteran larvae. *Ammophila marshi* exhibits a prey-nest-egg sequence and caches paralyzed prey low (generally ≤ 15 cm high) in plants during nest excavation. *Ammophila dysmica* and *A. azteca* excavate nests before capturing prey. Foraging ants in the genus *Formica* were abundant throughout the site and interfered with several aspects of wasp nesting activity, including nest-site selection, nest excavation, prey transport, and nest provisioning. Ants also occasionally preyed on adult wasps and raided completed nests. For more detailed descriptions of the study site and ant–wasp interactions see Rosenheim (1987, 1988).

Ant Foraging

Final-instar potato tuber moth larvae, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), reared on russet potatoes, *Solanum tuberosum* L., and killed by freezing were used as bait items in all ant foraging experiments. These baits were chosen for their similarity to the moth larvae used as provisions by *Ammophila* spp. Experiments were performed only during conditions of full sunlight.

Experiment 1. The first experiment compared ant foraging rates on ground and aerial baits. Five widely separated plots, each 5 × 2.5 m and consisting of 50 contiguous 0.25-m^2 subplots, were established in areas of *A. marshi* nesting activity. On 30 June 1985, 0600–0955 PDT, two baits were placed in each subplot, one on the ground and one suspended 3–15 cm high in grass clumps or other herbaceous plants. Aerial and ground baits were put out simultaneously in each subplot. The number of baits remaining in each plot was scored five times at 1- to 2-h intervals.

Experiment 2. The second experiment was designed to more accurately define the ant foraging rate on ground baits. On 31 June 1985 one bait was placed on the ground in 25 subplots of each of the five plots established for experiment 1. The number of baits remaining was scored at 2- to 15-min intervals for at least 60 min. The experiment was performed sequentially in plots 1–5 in the morning and then repeated in the afternoon, for a total of 10 replicates.

Forty ants foraging in plots 1–5 were sampled on 4 July 1985 to estimate ant species composition.

Experiment 3. The third experiment, performed 28 June 1988, provided a quantitative comparison of ant foraging rates on simultaneously presented aerial and ground baits. Five new plots, each consisting of 25 contiguous 0.25-m^2 subplots, were again established in *A. marshi* nesting areas. Twenty-five aerial baits were placed in a plot, immediately followed by 25 ground baits. The number of ground baits remaining was scored as rapidly as possible for the first 5 min and about every 5 min thereafter until none remained. The number of aerial baits was scored immediately after the last ground bait was removed and irregularly for the rest of the day.

A sample of approximately 20 ants retrieving ground baits on 4 July 1988 was collected at four of the plots to estimate foraging ant species composition.

Experiment 4. The fourth experiment was designed to quantify within-day variation in ant foraging activity. One plot that received continuous direct sunlight 0900–1800 was used. Twenty-five ground baits were set out hourly 0900–1800, and the number remaining scored as in experiment 3. A mercury thermometer placed on the soil surface and shaded except for the silver bulb provided measurements of surface temperatures. From three to five replicates were performed for each hour during 5–15 July 1988.

Statistical Analyses. The numbers of aerial and ground baits remaining in plots were compared with G tests of independence (df = 1). To summarize sequential scores of baits remaining within a plot, bait removal was modeled as an exponential decay,

$$N(t) = N_0 e^{kt} \tag{1}$$

where $N(t)$ is the number of baits remaining at time t, N_0 is the initial number of baits, and k is the rate of bait removal, which is assumed to be approximately constant. After taking natural logarithms, Eq. (1) reduces to

$$\ln N(t) = kt + \ln N_0 \tag{2}$$

Values of k were therefore obtained as the slope of a linear regression of $\ln N$ on t, with each observation weighted by N. The fit of the data to this model appeared to be good, with a mean regression coefficient, r, of 0.95 (SE = 0.0095; $n = 65$). Results of these experiments are presented using the more intuitive half-life time for baits, $t_{1/2}$, calculated as

$$t_{1/2} = \ln(0.5)/k \tag{3}$$

$t_{1/2}$ is the estimated time required for half of the baits to be removed.

Ant–Wasp Interactions

To determine if within-day fluctuations in ant foraging activity resulted in parallel fluctuations in the risk of ant interference with *Ammophila* spp. nesting activity, ant–wasp interactions were recorded during observations of nest construction and provisioning, made 0900–1800, 5 July–28 August 1983, 30 June–21 August 1984, 22 June–4 August 1986, and 22 June–17 July 1988. The numbers of successful nest excavations and provisionings were recorded as a measure of hourly wasp activity. Durations of nest excavations by *A. marshi* were also recorded to estimate the period of vulnerability for cached prey.

RESULTS

Experiment 1. Foraging ants removed ground baits substantially faster than aerial baits (Fig. 1A). The first census of experimental plots, performed 150–222 min after 50 aerial and ground baits were set out, revealed 16–34 aerial baits but no ground baits (Fig. 1A); bait position exerted a significant effect on bait removal rate (for plots 1–5, $G = 25.25–65.51$, $P < < 0.001$). A mean (±SE) half-life of 164.5 ± 35.4 min ($n = 5$; range, 114.0–302.9 min) was observed for aerial baits.

Experiment 2. Foraging ants removed ground baits rapidly (Fig. 1B); the mean ground bait half-life was 18.1 ± 12.5 min ($n = 10$). Substantial between-

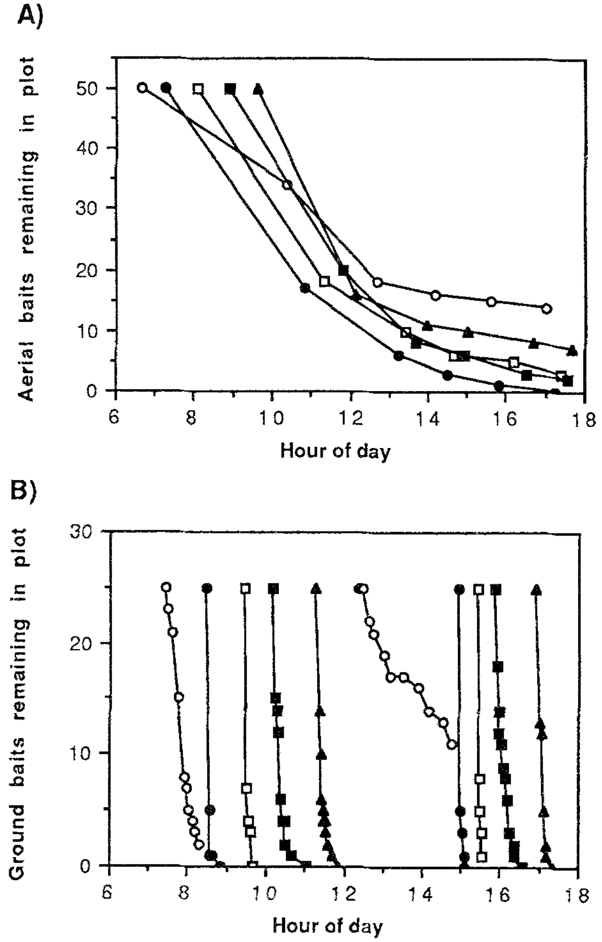

Fig. 1. (A) Experiment 1. Time course of foraging ant removal of aerial baits; shown are sequential replicates in plots 1 (open circles), 2 (filled circles), 3 (open squares), 4 (filled squares), and 5 (filled triangles). Ground baits had been completely removed by the time of the first census. (B) Experiment 2. Time course of foraging ant removal of ground baits; shown are 10 sequential replicates. Symbols same as in A.

replicate variability in rate of bait removal was observed ($t_{1/2}$ range, 2.0–130.0 min).

Forty ants foraging in the plots on 4 July 1985 were identified as *F. sibylla* (n = 33), *Formica subsericea* Say (n = 2), *Formica fusca* L. (s.l.) (n = 1), and *Tapinoma sessile* (Say) (n = 4, cooperating to remove one bait).

Experiment 3. As in experiment 1, ground bait removal rates greatly exceeded those for aerial baits (data not shown). From 8 to 19 of the original 25 aerial baits were counted in plots immediately after the last ground bait was removed, showing a significant effect of bait position (for plots 1-5, $G = 12.62$–38.86, $P < 0.001$). This comparison is conservative, since aerial baits were set out a mean of 9.0 min before ground baits. Mean half-lives of 126.9 ± 24.7 and 7.2 ± 2.1 min were observed for aerial and ground baits, respectively ($n = 5$ replicates each).

Seventy-eight ants foraging in the experimental plots for baits on 4 July 1988 were identified as *F. sibylla* ($n = 74$), *F. subsericea* ($n = 3$), and Myrmicinae sp. ($n = 1$).

Experiment 4. Within-day variation in ant foraging activity was pronounced, with bait half-lives increasing dramatically during the midday (Fig. 2). Although bait half-lives calculated for each experimental replicate were significantly positively correlated with soil surface temperatures measured at the beginning of the replicate (Spearman's $r = 0.584$, $n = 40$, $P < 0.001$), the daily peak in bait half-life did not coincide with the daily peak in temperature (Fig. 2).

Ant–Wasp Interactions. Ant interference with wasp nesting activities were

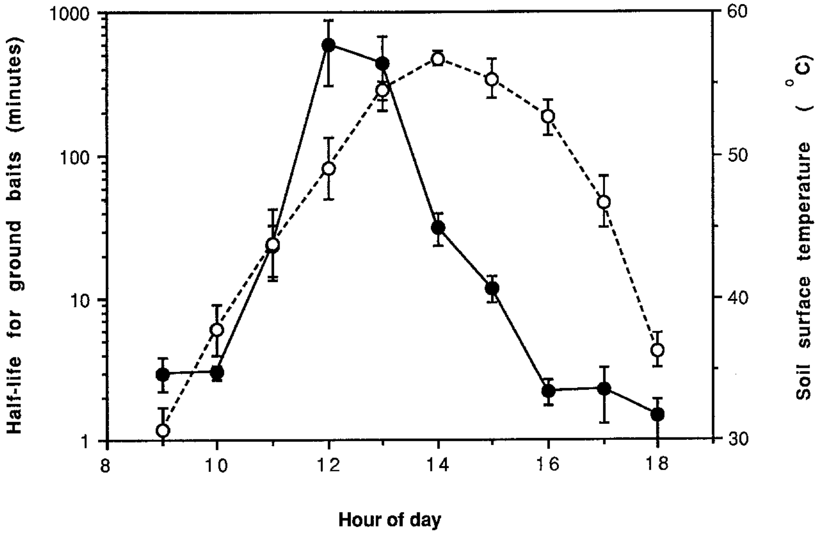

Fig. 2. Experiment 4. Within-day variation in ant foraging rate on ground baits, as expressed in bait half-lives (filled circles). Open circles are soil surface temperatures. Shown are means ± SE.

most commonly observed before 1100 and after 1500, paralleling observed cycles of ant foraging activity. Twenty instances of delayed nest abandonment, in which wasps permanently abandoned nests which had been under excavation for at least 5 min, were observed 1983–1988 for *A. dysmica* as an immediate response to ant interference. Of these 20, 3 occurred between 1100 and 1500 and 17 occurred earlier or later; 82 and 122 nests were successfully excavated during these time intervals, respectively, suggesting an effect of time on the probability of ant interference ($G = 5.57$, $P < 0.025$). Other forms of ant interference were observed too infrequently to produce statistically meaningful results, but suggested similar trends. Theft of provisions from *A. dysmica* occurred during 0 of 80 nest provisionings observed between 1100 and 1500 and 4 of 104 provisionings observed earlier or later. Two instances of ant penetration into nests provisioning, resulting in the destruction or removal of the nest contents, were observed, one during the midday and one later. Theft of aerially cached provisions of *A. marshi* was observed during 0 of 18 nest excavations occurring between 1100 and 1500 h and 2 of 25 excavations occurring earlier or later. Both instances of ant predation of adult *A. azteca* (one male and one female) were observed before 1100.

DISCUSSION

Although ants, primarily *F. sibylla*, foraged both on the ground and in plants, ground baits were harvested approximately ten times more rapidly than aerial baits. Nest excavation by *A. marshi* required an average of 22.4 ± 2.1 min ($n = 11$) in 1984. Assuming a nest excavation of 22.4 min and a half-life for ground baits of 14.5 min, the mean value observed for ground baits in experiments 2 and 3, Eq. (1) predicts that 65.8% of provisions cached on the ground would be stolen by ants during nest excavation. Assuming instead a half-life for aerial baits of 145.7 min, the mean observed for aerial baits in experiments 1 and 3, Eq. (1) predicts that only 10.1% of aerially cached provisions would be stolen. Thus aerial cache sites appear to provide a significant spatial refuge from ant predators. Theft of 2 of 42 (4.8%) aerially cached *A. marshi* provisions was observed during nest excavation in 1984. This observed value is less than that predicted from the ant foraging experiments (10.1%) but may underestimate ant predation since most nest excavations (31/42) were not observed in entirety, and thefts of provisions occurring before observations were begun would not have been recorded. The similarity of the experimentally predicted and observed rates of ant predation suggests that inferences from the ant foraging experiments may have some applicability to natural ant–wasp interactions.

In addition to the spatial refuge of aerial cache sites, the foraging experiments suggested a temporal refuge from ants during the midday (Fig. 2). This suggestion was supported by observations of ant interference with nesting activities of *Ammophila* spp., which occurred primarily during the early morning and late afternoon. A midday refuge from ants contrasts markedly with the impact of another natural enemy of *Ammophila* spp. at Sagehen Creek, the cleptoparasite *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), which was most active between 1200 and 1500 (Rosenheim, 1989). Thus, host wasps were faced with a trade-off between increased risk of ant interference during the morning and afternoon and increased risk of nest parasitism during the midday.

The weak association observed between bait half-life and soil surface temperature suggests two possible interpretations. First, thermal constraints may be shaping ant activity patterns, and the failure to document a closer relationship between the two variables may be related to the method of measuring temperature. Second, other factors which may influence ant foraging, such as variation in other abiotic conditions (e.g., solar radiation, humidity), resource availability, or the presence of interspecific competitors or parasitoids (Feener, 1988), may covary with temperature, confounding the interpretation of the observed association. Additional work is therefore required to assess the cause of the observed cycles of ant activity.

One aspect of aerial caching behavior not specifically addressed by the study is the tendency of many wasps, including *A. marshi*, to move prey from cache to cache as nest excavation proceeds (e.g., Evans, 1958; Alm and Kurczewski, 1984). One testable hypothesis is that this behavior might reduce theft of provisions by small ants, which may require recruited groups to transport discovered provisions. Small ants did not, however, appear to be important predators at Sagehen Creek. Frequent wasp returns to cached provisions might also provide for active defense against ants, including larger species like *F. sibylla* that can individually remove cached provisions.

Aerial caching of provisions is the norm for at least four of the five *Ammophila* spp. which exhibit prey-nest-egg sequences, including *Ammophila dolichodera* Kohl (Weaving, 1984), *A. marshi*, *Ammophila novita* (Fernald) (Ponder, 1976), and *Ammophila wrightii* (Cresson) (Hicks, 1934); *Ammophila boharti* Menke also excavates nests after capturing prey (unpublished data), but cache sites are unknown. Fragmentary observations of *Ammophila haimatosoma* Kohl suggest that it also may exhibit a prey-nest-egg sequence (Roth, 1928), but cache sites are again unknown. Use of aerial refuges from ants is not, however, limited to these species. *Ammophila stangei* Menke caches provisions aerially while removing the temporary closure from previously excavated nests (unpublished data). *Ammophila dysmica* may climb into plants while transporting provisions as an immediate response to contact with ants (Rosenheim, 1987). Thus, use of above-ground refuges from ants may be relevant to a broader array of nesting behaviors, including potential influences on the relative costs and benefits of ground versus aerial nest construction.

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