Parasite Presence Acts as a Proximate Cue in the Nest-Site Selection Process of the Solitary Digger Wasp, *Ammophila dysmica* (Hymenoptera: Sphecidae)

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Nest-site selection by the solitary ground-nesting wasp Ammophila dysmica *Menke was studied during 1982–1986 in California's Sierra Nevada Mountains. Digging females detected and discriminated among members of a complex of insect intruders, including a number of predators and parasites. In response to some natural enemies, wasps sometimes permanently abandoned nests under construction. These selective nest abandonments reduced the mean number of cleptoparasitic chrysidid wasps,* Argochrysis armilla *Bohart, attending the excavation of completed nests. The number of* A. armilla *attending a nest excavation correlated positively with the probability of nest parasitism by this species. Selective nest abandonment may reduce parasitism rates.*

INTRODUCTION

The proximate cues employed by insects to select habitats are extremely diverse and may be directly or indirectly related to fitness-modifying ecological factors (Prokopy and Owens, 1983; Miller and Strickler, 1984; Vinson, 1984). The role of predation and parasitism pressures in molding insect habitat selection is beginning to be uncovered (e.g., Kettlewell, 1973; Jaenike, 1985), along with the proximate cues used to assess an environment's predator or parasite load (Cooper, 1984; Sih, 1986).

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During an investigation of the behavioral ecology of the solitary, ground-nesting wasp *Ammophila dysmica* Menke (Hymenoptera: Sphecidae), frequent interactions with natural enemies were observed (Rosenheim, 1987a). *Ammophila* species excavate a series of separate unicellular nests and are, therefore, repeatedly faced with nest-site selection decisions. Here I describe the nest-site selection process of *A. dysmica* and present evidence suggesting that these wasps are cued by the presence of natural enemies.

METHODS AND EXPERIMENTAL RATIONALE

I investigated nest-site selection during a study (1982–1986) of *A. dysmica* and associated parasites at the Sagehen Creek Field Station, Nevada County, California. The study site was on a broad ridgetop, elevation 2000 m, that had been deforested by a 1960 fire [see Rosenheim (1987a) for a detailed description of the area]. *A. dysmica* nested both as isolated individuals and in aggregations, often along a dirt road that traversed the site. Nesting aggregations were monitored daily, 0900–1800 h Pacific Daylight Saving, throughout the nesting season from late June to early August. Observations of nest-site selection, nest excavation, nest abandonment, and interactions with conspecific wasps and an array of parasites and predators were recorded.

Argochrysis armilla Bohart developed as a cleptoparasite in *A. dysmica* nests. This parasite was chosen for detailed study because (i) it was the principal mortality factor of *A. dysmica*, achieving annual parasitism rates of 21.3–43.5% (1983–1986) (Rosenheim, 1987a), and (ii) its strategy of host exploitation suggested that *A. dysmica* would be under strong selective pressure to avoid excavating nests in microhabitats (i.e., nest sites) that the parasite had discovered. *A. armilla* located host nests during nest excavation; nests under construction were, however, relatively invulnerable to parasite oviposition. Parasites learned the location of nests, enabling them to monitor nest sites while the host searched for caterpillars (Rosenheim, 1987b). Parasites could then return to oviposit in the nest when the host returned with provisions. The probability of nest parasitism rose from 7 to 60% as the number of *A. armilla* discovering the nest during excavation rose from 0 to ≥3 (Table I).

My criterion for considering a nest site to be *selected* was the complete excavation of a nest (and see Brockmann, 1979). I considered a site *investigated and rejected* if ≥5 min of digging was followed by permanent abandonment. To compare selected sites to rejected ones, I measured the number of *A. armilla* attending each nest excavation. An *attending* parasite faced the digging wasp from perches within about 30 cm of the nest entrance. Parasite abundance for each nest, completed or abandoned, was scored as a function of time in the following manner: (1) nests started with a score of 0 at the initiation of digging;

(2) the score remained 0 until a parasite was attracted to the digging wasp and began nest attendance, then increased to 1; and (3) the score remained 1 (even if the parasite departed) until two parasites attended the nest simultaneously, then increased to 2. This process was continued until the nest was completed or abandoned. The parasite abundance score for each nest plotted against time was an increasing step function. Average parasite abundance "curves" for (i) completed ($N = 105$) and (ii) abandoned ($N = 89$) nests were constructed by averaging these step functions across all nests. Parasites were not aggressive toward one another.

Two-sample Wilcoxon tests (test statistic reported as t_s and corrected for ties of rank) were used to compare means. Frequency data were analyzed with G tests of independence.

RESULTS

Home-Site Fidelity. A. dysmica nesting in the study area formed several loose aggregations which persisted in the same locations from 1982 to 1986. The aggregation studied in 1986 had a density of 159 nests/150 m². Marked females constructed successive nests within the same nesting area; the average distance between successive completed nests was 5.3 ± 7.7 m (range, 0.03–27 m; $N = 23$).

Nest-Site Searching Behavior. Females searching for a place to initiate digging interspersed low flights with searching on foot. While walking the body was tilted forward, with the head almost touching the ground and the antennae tapping the soil surface. Nest sites selected were in open, level, relatively bare areas that received direct sunlight for most of the day. The soil was friable, well drained, and low in coarse plant material.

Table I. The Relationship Between *Ammophila dysmica* (Host) Nest Outcome and *Argochrysis armilla* (Parasite) Abundance During Nest Digging[a]

Nest outcome	Parasite abundance during digging			
	0	1	2	3–5
Parasitized	1	6	10	9
Unparasitized	14	14	16	6

[a] Parasite abundance scored as the maximum number of parasites present simultaneously at any time during nest excavation. Nest outcome is not statistically independent of parasite abundance ($G = 11.03$, $P < 0.02$).

Wasps responded to conspecific nests while searching for nest sites. A similar response occurred irrespective of whether the nests were fully excavated or abandoned, active or completed, open or closed, or belonged to the searching female or some other wasp. Females generally paused briefly at conspecific nests, antennated the closure, and then collected one to several pebbles which were dropped onto the closure. Occasionally a closure was partially removed and then replaced. The raiding of nests (Rosenheim, 1987a) may have been an extension of these behaviors. The recognition of nests may have been partially visual, as small craters of the ant *Formica sibylla* W. M. Wheeler were occasionally also inspected and given pebbles.

Nest-Site Abandonment. Females generally dug and abandoned a number of sites before digging a complete nest. Most abandonments occurred after a brief (<1-min) period of digging. A continuum of behaviors existed between searching, biting the ground one to a few times, and these abandoned diggings. More extensive excavations were also abandoned (Fig. 1); the results presented below concern these delayed abandonments—those occurring after ≥5 min of digging.

The probability of delayed nest abandonment decreased with increasing time spent digging ($G = 107.7$, df = 6, $P ≤ 0.001$). There did not appear to be an absolute time of commitment after which nests were always completed;
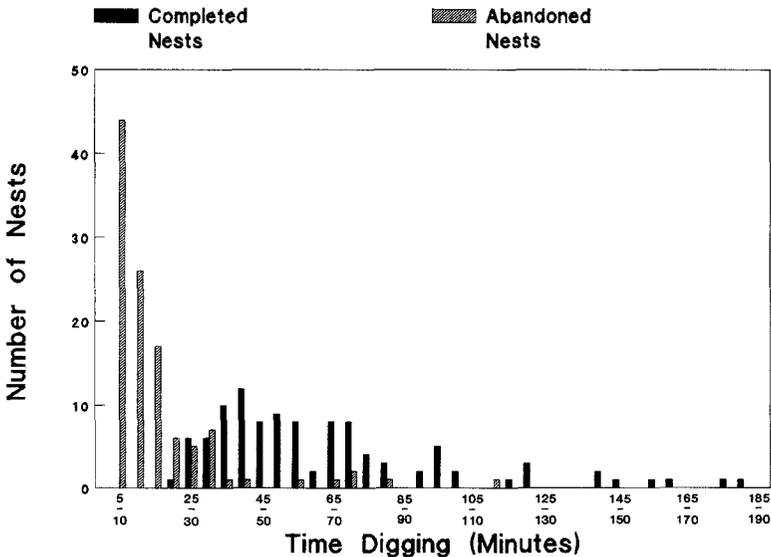

Fig. 1. Durations of *Ammophila dysmica* digging activity at 113 abandoned and 105 completed nests (5-min increments).

rather, the propensity to quit a site decreased gradually (Fig. 1). In response to an ant bite one female abandoned a completely excavated nest that she was trying to close, indicating that there was also no absolute commitment relative to the stage of nest excavation. Females placed rudimentary closures on abandoned nests by dropping a series of loose pebbles or other soil surface debris into the burrow.

Field observations suggested possible causes of nest abandonments. Interactions between digging females and other insects were common. Many intruding insects did not elicit nest abandonments (Table II); the presence of these insects during nest excavation did not represent a threat to the nest. Although the cleptoparasitic fly *Hilarella hilarella* Zedterstedt did develop in about 3% of *A. dysmica* nests (1983–1986), larviposition occurred exclusively during nest provisioning, and these flies did not appear to learn the location of discovered nests (Rosenheim, 1987a). Interactions with natural enemies whose presence during nest construction indicated an immediate or eventual threat to the nest (see Rosenheim, 1987a) did, however, sometimes result in nest abandonment (Table II). Females responded aggressively to the detection of conspecific females, ants, *Formica* spp., and *A. armilla*, all of which were pursued in flight and bitten. In contrast, females responded to hovering, ovipositing bombyliid flies, *Exoprosopa dorcadion* Osten Sacken, by "freezing" for up to 3 min until

Table II. Interactions Between Nest-Digging *Ammophila dysmica* and Other Insect Inhabitants of the Nesting Area and the Resulting Impact on Nest Abandonment[a]

Intruder	Frequency	Threat	Inducing immediate nest-site abandonment[b]
A. dysmica female	Rare	?	Never observed
A. dysmica male	Very common	No	Never observed
Asilid fly	Occasional	No	Never observed
Hilarella hilarella (Diptera: Sarcophagidae)	Occasional	No	Never observed
Formica spp. ant (mainly *F. sibylla*)	Very common	Yes	Common (16/113)
Exoprosopa dorcadion (Diptera: Bombyliidae)	Occasional	Yes	Common (8/113)
Argochrysis armilla (Hymenoptera: Chrysididae)	Common	Yes	Common (9/113)

[a] Intruders were considered to represent a threat if their presence during nest excavation indicated an increase in the risk of (i) nest parasitism during nest excavation or provisioning or (ii) theft of provisions during nest provisioning.

[b] Figures are the number of nest abandonments induced by the specified intruder/the total number of nests abandoned during 1986. Only nests abandoned immediately following the interaction with the intruder are tallied.

the parasite departed. *E. dorcadion* appeared to locate nests by responding to visual cues generated by the movements of digging *A. dysmica*; freezing appeared to remove the attractive stimulus, resulting in the parasite's departure. Of 14 nests into which *E. dorcadion* oviposited (1983–1986), 10 were abandoned. Table II reports only the most obvious impact of natural enemies on nest-site selection: the immediate abandonment of 33 nest sites following aggressive interactions. Parasites and predators may have contributed in less obvious ways to the remaining 80 abandonments observed in 1986.

The observations of nest abandonment indicated (1) that *A. dysmica* was capable of differentiating between a number of intruders at the nest and (2) that, in at least some cases, the acceptance or rejection of nest sites could depend upon the presence of natural enemies. However, many nests were completed in the presence of these same natural enemies, even after they had been detected. Furthermore, 80 of the 113 (71%) abandonments did not occur as *immediate* responses to natural enemy detection. Thus, a larger question remained: Did the entire class of delayed abandonments reduce the number of natural enemies attending nest excavations? The presence of *E. dorcadion* at 9 of 113 abandoned and 4 of 105 completed nests (1986) was suggestive but inadequate to provide a statistically meaningful answer to this question ($G = 1.724$, $P > 0.10$).

Influence of Argochrysis armilla *on Nest Abandonment*. Nest abandonments reduced the mean number of *A. armilla* attending nest excavations. The average *A. armilla* abundance score for 105 completed and 89 delayed abandoned nests is plotted versus time in Fig. 2. (Twenty-four nests abandoned due to ant or bombyliid presence were excluded to reduce variation not due to *A. armilla*.) The plots display parasite scores through 18 min, when the number of active nests in the abandoned nest sample fell below 20 (Fig. 1). The two classes of nests began with similar scores, but abandoned nests had accumulated a greater average parasite score by 2 min and remained at a higher level throughout the next 16 min, during which 78% of all delayed abandonments occurred. The difference between the completed and the abandoned nest samples was statistically significant at 6, 7, and 11 min ($t = 1.85$, 1.92, and 1.69; $n = 105$; $N = 84$, 70, and 51, respectively; $P < 0.05$), marginal at 12 min ($t = 1.48$; $n = 105$; $N = 45$; $P < 0.07$), and nonsignificant at 5, 8, 9, and 10 min ($t = 0.98$, 1.26, and 0.92; $n = 105$; $N = 89$, 62, 60, and 55; $0.11 < P < 0.19$). After 12 min the differences between the curves were nonsignificant, in part due to the declining abandoned nest sample size (Fig. 1). Thus, a difference between the two samples is discernible but subtle; the effect of *A. armilla* is partially obscured by the unexplained variation due to the effects of other parasites, predators, and variable substrate characteristics. The decision to abandon a nest does, however, appear to be selective.
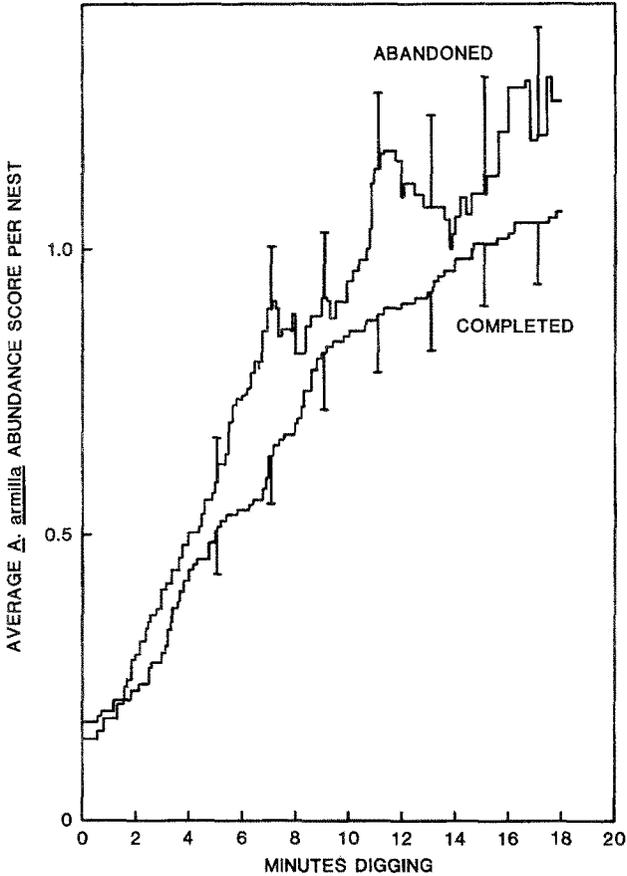
Fig. 2. Average *Argochrysis armilla* (parasite) abundance score per *Ammophila dysmica* (host) nest for a sample of 105 completed nests (shown with one negative standard error of the mean) and 89 delayed abandoned nests (shown with one positive standard error).

DISCUSSION

Quantitative ecological studies of solitary nesting wasps have demonstrated that nesting success is often greatly reduced by parasites and predators (e.g., Freeman and Parnell, 1973; Freeman and Taffe, 1974; Freeman and Jayasingh, 1975; Taffe and Ittyeipe, 1976; Peckham, 1977; Freeman, 1982; Spofford *et al.*, 1986; Rosenheim and Grace, 1987). Furthermore, the impact of natural enemies has been found to be nonuniform across varying environments. Para-

sitism rates may vary with nest density (Freeman and Parnell, 1973; Freeman and Taffe, 1974; Freeman and Jayasingh, 1975; Freeman, 1982; Wcislo, 1984), nest substrate (Taffe and Ittyeipe, 1976; Endo, 1980), and vegetational coverage (Endo, 1980). Nonetheless, studies of nest-site selection have generally not considered the possible use of natural enemy abundance as a proximate basis for nest-site evaluation. Instead workers have focused, with considerable success, upon site selection as a response to an environment's abiotic and biotic structural characteristics (Brockmann, 1979; Rubink, 1979; Toft, 1987) and the distribution of conspecific females (Rubink, 1982; Larsson, 1985) and males (Evans *et al.*, 1986). The importance of philopatry has also been elucidated (Brockmann, 1979; Toft, 1987).

In the first attempt to understand the role of natural enemies in nest-site selection by a solitary wasp, Endo (1980) showed that pompilid wasps shifted digging sites in response to the presence of parasitic flies. The result of moving to a new site was a slightly increased probability of constructing the nest in the absence of parasites; the increase was not evaluated for statistical significance. Endo (1980) interpreted his results narrowly, suggesting that the ability to shift nest sites was linked to the host's primitive nesting behavior of capturing prey before excavating the nest (a prey–nest sequence).

The results of the current study extend the conclusions of Endo (1980) to a system involving a complex of natural enemies and a nest–prey behavioral sequence. *A. dysmica* detected and exhibited specific responses to intruders at the nest. While contacts with conspecific males and females, asilid flies, and *H. hilarella* did not elicit nest abandonments, contacts with ants, *E. dorcadion*, and *A. armilla* (those intruders whose presence represented a short- or long-term threat to the nest) did provoke abandonments. On logical grounds, it seems likely that the abandonment of nest sites in direct response to natural enemy presence increased the likelihood of constructing a nest in an area of low natural enemy abundance, thereby reducing the impact of parasites and predators.

By removing the most heavily parasite-attended nest sites from the total sample of nest excavations, the entire class of delayed abandonments was found to reduce the average number of the key parasite, *A. armilla*, attending nest excavations. Because the probability of nest parasitism was positively correlated with the number of parasites attending the nest's excavation (Table I), this decrease appears likely to have produced a parallel decrease in the final rate of nest parasitism. The small magnitude of the observed effect of *A. armilla* on nest abandonment (Fig. 2) may be partly attributable to the parasite's nest-attending behavior. Parasites watched nesting females from nearby perches where they remained motionless while the host was above ground, flying from perch to perch or to the nest entrance only when the host was in the cell below. *A. dysmica* was able to detect *A. armilla* only if they moved; stationary cleptoparasites observing the nest from nearby perches were therefore effectively

invisible. Only when *A. armilla* were induced to move in the presence of the host by interactions with hetero- and conspecifics, including male mating attempts and incidental contact with other females attending the nest, were they perceived and pursued in flight by the host (Rosenheim, 1987).

In a seminal paper, Brockmann (1979) suggested that nest-site selection in the ground-nesting wasp *Sphex ichneumoneus* L. was a hierarchical process in which the wasp made sequential decisions of (1) when to dig, (2) where to search, (3) where to bite, and (4) where to dig. Wasps answered the question of where to dig by sampling the soil surface temperature and consistency during the initiation of burrow digging. Nest-site selection by *A. dysmica* appears to be well described by such a hierarchical model but suggests the addition of a fifth decision level: where to *complete* a nest. By not committing early to a site, *A. dysmica* was able to use the early period of nest construction as a passive means of sampling the nest site's immediate parasite and predator load. Abandonment of nest sites after substantial excavation appears to be widespread in the ground-nesting Hymenoptera (Brockmann and Dawkins, 1979); thus decisions of where to complete a nest may be important to many species. The present study has, however, only begun to look at the cues which may be relevant to the determination of where to complete a nest. Further study will be required to understand more fully the information integrated by *A. dysmica* and other ground-nesting Hymenoptera both before and during nest excavation to make nest-site selection decisions.

ACKNOWLEDGMENTS

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