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Host location and exploitation by the cleptoparasitic wasp *Argochrysis armilla*: the role of learning (Hymenoptera: Chrysididae)

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Summary. The nesting behaviors of many solitary ground-nesting wasps incorporate temporal barriers against would-be cleptoparasites. Nests being excavated are conspicuous but relatively invulnerable to parasites, while nests being provisioned, often several hours to days later, are inconspicuous but highly vulnerable. *Argochrysis armilla*, a cleptoparasite of solitary ground-nesting wasps, *Ammophila* spp., bridges the temporal gap between nest excavation and provisioning by (i) visually locating digging hosts, (ii) learning the locations of associated nests, (iii) maintaining surveillance on a series of nests during the hosts' absence, and (iv) ovipositing in nests when the host returns with provisions. Patterns of surveillance and parasitism of *Ammophila dysmica* nests were generated by the number of cleptoparasites discovering and learning the nest's location during excavation. These results support recent suggestions that learning may play an important role in shaping foraging strategies of insect parasites.

Introduction

Early comparative ethologists used landmark displacement techniques to establish the ability of solitary digger wasps to learn the "topography" of their nest-site and thereby relocate previously constructed nests (van Iersel 1975). Locality learning enabled solitary ground-nesting wasps to change their nesting behavior from the primitive prey-nest sequence, in which the nest is excavated after the provisions are collected, to the more advanced nest-prey sequence, in which the frequently lengthy hunting process begins after the nest is dug (Evans 1958). This reordering avoids the risk of theft or parasitism of the provisions during nest excavation (Evans 1977); but it is also significant in temporally separating the stage of the nesting cycle that is most conspicuous to parasites, nest digging, from the stage that is most vulnerable to exploitation, nest provisioning (Rosenheim 1987a). In this way host behavior challenged potential cleptoparasites to bridge the temporal gap between nest excavation and nest provisioning. Here I present experimental results for one cleptoparasite, *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), that has adapted to this temporal gap; *Argochrysis armilla* (i) orients visually to digging hosts, (ii) learns the locations of associated nests, (iii) attends a series (or "trapline") of nests for up to several days while the host hunts for provisions, and (iv) successfully oviposits in attended nests during nest provisioning. Observations of a nesting aggregation of *Ammophila dysmica* Menke (Hymenoptera: Sphecidae) revealed the significance of the learned foraging strategy in generating patterns of nest surveillance and parasitism. This study is the first demonstrating a strategy of host exploitation based upon locality learning by an insect parasite and supports recent suggestions of the importance of learning in insect foraging (Papaj and Rausher 1983; Gould 1985, 1986; Menzel 1985; Lewis 1986; Papaj 1986; Jermy 1986).

Methods

Argochrysis armilla was studied from 1982–1986 at Sagehen Creek Field Station, Nevada County, California, USA, where it developed as a cleptoparasite in the nests of solitary ground-nesting wasps of the genus *Ammophila*. The study site was located on a broad ridgetop, elevation 2000 m, where *Ammophila* spp. nested in several aggregations along a dirt road. *Ammophila* provision unicellular nests with one to several lepidopteran larvae, and both species discussed here, *Ammophila dysmica* and *Ammophila azteca* Cameron, exhibited nest-prey behavior patterns. *Argochrysis armilla* achieved annual parasitism rates of 21.3–43.5% in nests of *Ammophila dysmica*, despite the fact that nest provisioning occurred an average of 10.4 ± 8.5 h after nest excavation ($n = 128$) (Rosenheim 1987a). No other parasites achieved parasitism rates in excess of 4%. For a more detailed description of the site, the nesting behavior of *Ammophila dysmica*, and interactions of *Ammophila dysmica* with *Argochrysis armilla* see Rosenheim (1987a).

Parasite surveillance of host nests

The abundance of *Argochrysis armilla* attending *Ammophila dysmica* nests was assessed during three stages of the nesting cycle by scoring the maximum number of parasites present simultaneously at any time during the sampling period. Parasites were considered to be in attendence if they landed on or hovered directly above the nest entrance, or if they perched at least twice sequentially facing the nest entrance from a distance of less than 30 cm. The period of nest digging was monitored to yield the first sample; nest digging required an average of 63.5 ± 35.6 minutes ($n = 102$). During the absence of the hunting wasp, 3-min nest surveys were performed hourly during the period of high parasite activity, 1100–1600 h. These surveys were made for five days after nest excavation or one day after the completion of nest provisioning, whichever occurred first. Finally, parasite abundance was monitored during the period of the nest's greatest vulnerability, when the nest closure had been removed by the host wasp to deposit the caterpillar provision, oviposit, clean the nest, and find a pebble with which to re-plug the nest. The duration of this period averaged 185.7 ± 130.3 s ($n = 50$). Because *Argochrysis armilla* quit the nest-site after ovipositing in a host nest, the parasite abundance score during provisioning was slightly modified: if the maximum number of parasites simultaneously present was observed after n parasites had oviposited and departed, the score was increased by n.

At the end of the nesting season all *Ammophila dysmica* nests were excavated and scored as parasitized (*Argochrysis armilla* cocoon(s) present) or unparasitized (host cocoon present); nests whose contents were destroyed by mold or other parasites or predators were not included in the analysis.

A sample of *Argochrysis armilla* was marked individually with enamel paints spotted onto the thoracic dorsum ($n = 47$). The identity of these individuals could be determined without disturbance in the field.

Host location

Digging *Ammophila dysmica* were rapidly discovered by *Argochrysis armilla*, most nests being attended by one or more parasites within the first 10 min of digging (Rosenheim 1987b). To determine if parasites were using visual cues to orient to digging wasps, an artificial *Ammophila* lure was employed in an attraction experiment. The lure consisted of a dead female *Ammophila azteca* sealed in a coat of clear nail polish and suspended from a pole by a clear line. Fifty circular plots, each 0.5 m in diameter, were established along a 25 m transect of a nesting aggregation and randomly assigned to either the experimental (lure manipulated to simulate digging movements) or control treatment (no lure). Treatments were applied for ten minutes during which parasite abundance (scored as the maximum number of parasites simultaneously present) and the duration of the presence of ≥ 1 parasite within the plot was recorded.

Locality learning

A landmark displacement experiment was performed to investigate the mechanism of parasite orientation to nests during the host's absence. Observations made before this experiment had indicated that only parasites that had discovered a nest during excavation were able to reorient to the nest in the host's absence (see below). *Ammophila azteca* initiating nest excavations were surrounded by four artificial landmarks (white plastic LEGO® blocks, 32 × 16 × 19 mm with eight small cylindrical knobs on the upper surface) each placed 3 cm from the nest entrance in a square array. These landmarks remained in place for the duration of the digging. The presence and identity of marked *Argochrysis armilla* as well as the presence of unmarked parasites attracted to the nest were recorded. Parasite identity was recorded as a means of (i) distinguishing between initial and subsequent visits and (ii) increasing the replicate number, since only the first return of an unmarked parasite could be scored as an initial return, and all subsequent visits by any unmarked parasites had to be lumped in the total visits column. At the conclusion of the nest excavation the host and parasites generally departed. If all *Argochrysis armilla* had not departed within ten minutes, those remaining were flushed from the nest. Two false nests, each consisting of a short vertical tunnel provided with a single loose-fitting pebble closure similar to that of *Ammophila azteca*, were then constructed 6 cm from, and on opposite sides of, the true nest. The artificial landmarks were then removed. A coin flip determined which of the two false nests would be surrounded by an identical array of clean artificial landmarks. During the following hour, or until the return of the host, returns of *Argochrysis armilla* to members of the nest array were scored when parasites hovered directly over or landed on a nest. The scoring method was chosen because it was unambiguous and avoided the possibility of false positive scores associated with attraction to the LEGO® blocks independent of their role as landmarks. Twelve trials were conducted from 1 July 1986 to 14 July 1986.

Results

Host Location

The manipulated *Ammophila* lure employed in the attraction experiment increased both the number of *Argochrysis armilla* and the duration of their stay in the experimental plots (Table 1). Parasites were observed to reposition themselves on their perches to continue facing the moving lure. *Argochrysis armilla* searching within the nesting aggregation detected the moving lure only if they were perched nearby (maximum distance of detection appeared to be ca. 0.5 m) and were facing approximately towards the lure. Parasites moving past the lure in low cruising flights were not arrested, a result confirmed by observations of digging *Ammophila*. Although this experiment has not ruled out complementary roles for chemical or other cues, visual cues appeared to be sufficient to mediate initial host location by *Argochrysis armilla*.

These results alone did not, however, explain the observed rates of nest parasitism. Nests under construction were not generally vulnerable to *Argochrysis armilla*; parasites successfully penetrated the nest (a prerequisite of oviposition) during only

Table 1. *Argochrysis armilla* abundance and time present in plots (s.) with and without a manipulated *Ammophila* lure

Treatment	Parasite abundance score (mean time present per plot)		
	0	1	2
No lure	19	6	0
	(–)	(8.9 ± 5.0 s)	(–)
Lure	6	10	9
	(–)	(103.6 ± 63.4 s)	(246.8 ± 131.3 s)

Parasite abundance and time present, lure vs. no lure, $t_s = 4.01$, $P < 0.001$; and $t_s = 4.16$, $P < 0.001$, respectively, Wilcoxon 2-sample test

3 of the 109 *Ammophila dysmica* nest excavations observed in 1986. Eggs deposited in nests being dug would likely have been quickly discarded with excavated dirt. The parasites' strategy of host exploitation therefore had to extend beyond the initial nest discovery.

Individually marked parasites were commonly observed perching around and investigating the closures of nests while the host was away hunting for provisions. These nest-attending parasites were present at a nest only intermittently during the day; they also returned to nests from their nightly sleeping aggregations for up to 5 days after the nest excavation. Fifty-eight observations of marked parasites attending nests in the absence of the host were made for nests ($n = 18$) at which the identity was known of all marked parasites that had discovered the nest during the digging stage. Without exception, nest-attending parasites had also been present earlier during nest digging. Thus, prior experience appeared to be a prerequisite of reorientation to nests in the host's absence. In addition, parasites leaving newly discovered nests for the first time displayed stereotyped circling flights centered on the nest entrance (Fig. 1). Finally, it was parasites present at the nest when the host returned with provisions that produced the 21–43% parasitism rates observed; *Argochrysis armilla* oviposited during 32 of 94 (34.0%) *Ammophila dysmica* nest provisionings observed in 1986.

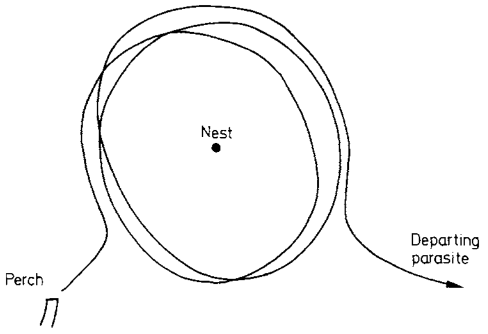

Fig. 1. *Argochrysis armilla* orientation flight. Circling flight was rapid and close to the ground (< 5 cm). Variable aspects included the diameter of the circles (usual range ca. 10–100 cm, rarely up to 180 cm) and the number of circles flown (usual range ca. 1–5, rarely up to 12)

Table 2. Landmark displacement experiment. Presented are individual parasite returns to members of an experimental array of nests including: (i) the true nest, (ii) a false nest surrounded by landmarks displaced from their former positions around the true nest, and (iii) a false nest without landmarks

	Nest visited				
	(i) True nest		(ii) False nest with landmarks		(iii) False nest without landmarks
First return	4	n.s.	12	***	0
Second return	1	n.s.	7	*	0
Total returns	9	***	44	***	1

Exact binomial probabilities were calculated. Following Bonferroni's inequality for 2 pairwise comparisons for each class of returns, differences were considered non-significant (n.s.) if $P > 0.025$; *: $P < 0.025$; ***: $P < 0.0005$

Locality learning

Parasites returning to the 3-nest array of the landmark displacement experiment made a significantly greater number of first, second, and total returns to the false nest surrounded by the displaced landmarks than to the false nest without landmarks (Table 2). Parasites also made a significantly greater number of total returns to the false nest surrounded by the landmarks than to the true nest. Marked parasites not present during the nest digging did not score any positive visits. All visits of individual parasites were made to the same nest, suggesting that parasites visiting the false nest were not alerted to their mistake by the absence of cues normally associated with a true nest. This contrasted with the behavior of the host wasps, who chose the false nest surrounded by the landmarks in 5 of 6 instances, but in 3 of these 5 cases quickly shifted to the true nest after briefly antennating the false nest's closure. Thus, the parasites appeared to return to the nest by using a learned knowledge of the nest site's topography, including the location of the nest relative to the artificial landmarks.

Parasite surveillance of host nests

Field observations of marked *Argochrysis armilla* explained the intermittent nature of nest surveil-

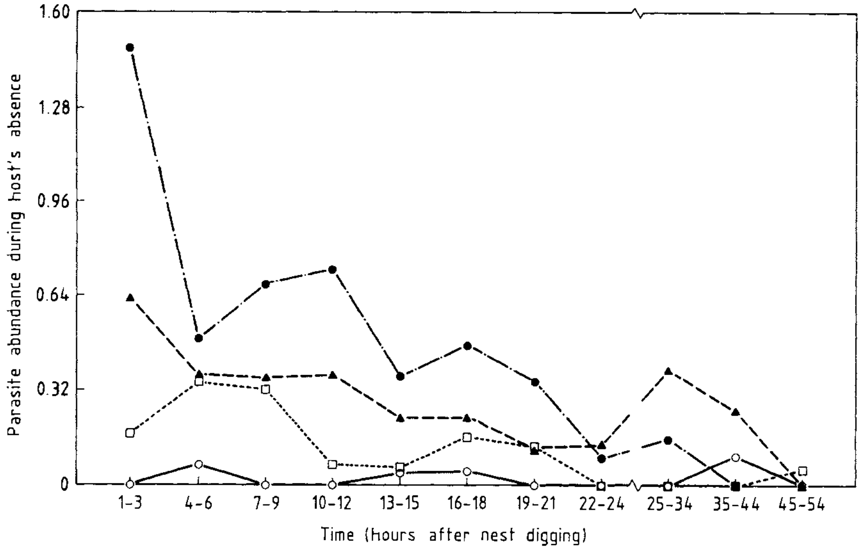

Fig. 2. Nest surveillance by *Argochrysis armilla*. Average parasite abundance scores during the host's absence plotted versus time since the completion of nest digging. Time calculated using the 9-h day of *Ammophila dysmica* activity. Nests grouped by their parasite abundance scores during digging: *closed circles* score of 3–5 ($n=21$); *triangles* score of 2 ($n=35$); *squares* score of 1 ($n=27$); *open circles* score of 0 ($n=22$). *Each point* represents an average of 5–21 observations

lance. Individual parasites were observed to interrupt their surveillance of one nest to fly to another active nest, where they would perch or inspect the closure for a variable time and then either return to the first nest or fly off to a third. Preliminary observations revealed parasites travelling as far as 42 m to traverse a trapline of up to 4 nests.

To relate the strategy of host exploitation exhibited by *Argochrysis armilla* to the ecological impact of this parasite upon *Ammophila dysmica*, parasite abundance during nest excavation was compared to parasite abundance during later stages of the nesting cycle and to the final nest outcome. Patterns of nest surveillance by *Argochrysis armilla* during the host's hunting period are presented in Fig. 2. The apparent trends were tested for statistical significance in the following way: (i) each nest's parasite abundance scores during the host's absence (y) were plotted versus time (x), (ii) a least squares line was fitted to each plot, (iii) the y-intercept and slope of these lines were then tested for correlation to the nest's corresponding parasite abundance score during digging. Nests with higher parasite abundance scores during digging had larger parasite abundance scores during the host's absence (Spearman's rank correlation; $r_s=0.524$, $P<0.001$), these scores declining more rapidly with time ($r_s=-0.218$, $P<0.02$). Parasite abundance scores during the critical stage of nest provisioning were also correlated with parasite abundance during excavation ($r_s=0.287$, $P=0.05$). Nests with parasite abundance scores during digging of 0, 1, 2, and 3–5 had parasite abundance scores during provisioning (mean ± SD) of 0.57 ± 0.98 ($n=7$), 0.70 ± 0.95 ($n=10$), 1.52 ± 2.32 ($n=21$), and 1.22 ± 1.39 ($n=9$), respectively. Nest outcome was also strongly related to the parasite abundance score during digging, with the probability of nest parasitism rising from 7% to 60% as parasite abundance during digging rose from 0 to ≥ 3 (Rosenheim 1987b). Thus, it was variation in the number of parasites discovering nests during excavation that generated the observed patterns of nest surveillance during the host's absence, parasite presence during nest provisioning, and nest parasitism. The ability to learn the location of discovered nests and thereby reorient to nests in the host's absence enabled *Argochrysis armilla* to bridge the temporal gap between nest digging and nest provisioning. The incorporation of several nests into a trapline may have increased the efficiency of the nest-attending process.

Discussion

The landmark displacement experiment distinguished between two possible mechanisms of *Argochrysis armilla* reorientation that incorporated the observed role of prior experience with the nest, i.e., that (i) parasites deposited a chemical mark on or near nests to which they could subsequently orient, or (ii) that parasites learned the nest's location. The preference of parasites for the false nest surrounded by the displaced landmarks indicates that a learned knowledge of the nest's location is the primary means of orientation in the immediate vicinity of the nest. The observed returns to the true nest may be attributable to the abundant naturally occurring landmarks, such as rocks or grass clumps, as well as possible chemical cues which may have competed with the artificial landmarks for the parasite's attention.

Many elements of the foraging and host utilization strategies of insect parasites may be modified by experience. Parasites may learn novel responses to visual or chemical cues associated with the host or host's microhabitat (Taylor 1974; Arthur 1981; Vet and van Opzeeland 1984; Wardle and Borden 1985) and may also learn to discriminate between parasitized and unparasitized hosts (van Lenteren 1981). Locality learning has not, however, been previously demonstrated for an insect parasite. Observations of foraging by members of several genera of cleptoparasitic bees do, however, suggest that locality learning may be widely employed as a means of returning to host nests (Linsley and MacSwain 1955; Rozen et al. 1978; Eickwort and Abrams 1980; Cane 1983). Parasitic bees perform circling "orientation" flights around host nests, travel between multiple nests, and return to previously located nests. Whether the basis for these behaviors is a learned knowledge of nest location is not known. Because parasitic bees evolved recently from groups of nest-building bees (Bohart 1970), their putative locality learning ability probably preceded their parasitic habit. Learning therefore may explain the observed patterns of cleptoparasitic bee foraging.

Locality learning for *Argochrysis armilla* appears in contrast to be a trait derived within the Chrysididae. The Chrysidoidea, comprising the Plumariidae, Scolebythidae, Sclerogibbidae, Embolemidae, Dryinidae, Bethylidae, and Chrysididae, diverged early from the evolutionary lineage of the aculeate Hymenoptera, forming a monophyletic sister group to the remaining Aculeata (Brothers 1975; Carpenter 1986). Host searching within a wood or soil substrate appears likely to have been the primitive habit for the Aculeata and the Chrysidoidea (Rasnitsyn 1980; Carpenter 1986). This habit appears to be retained by the primitive chrysidoid families, the Plumariidae and Scolebythidae, and is an unlikely setting for the evolution of locality learning as a foraging strategy, due to the constraints on vision. Only within the bethylid genus *Epyris* do we find nest building in the Chrysidoidea (Rubink and Evans 1979); in this case the nest is excavated after capturing the single prey, and the prey is carried by the nest-site searching wasp, eliminating the need for a learned knowledge of the nest's location. Thus locality learning, within either the context of foraging or return to a nest, is unknown within the Chrysidoidea exclusive of *Argochrysis armilla*. Based upon parsimony alone, the learning ability of *Argochrysis armilla* appears therefore to be a trait derived within the Chrysididae. Hosts excavating nests before capturing prey and hosts constructing multicellular nests may have generated significant selection pressures favoring the locality learning trait.

Locality learning and/or traplining has been described in a wide array of insect groups, including pollinators, herbivores, nest-builders, species using territorial or lekking mating systems, species sleeping in aggregations (Wehner 1981), and now in a parasite, *Argochrysis armilla*. The common ecological factor underlying the adaptive significance of this learning behavior in these groups appears to be the need to return to temporally stable and spatially heterogeneous resources (Baker 1978). These are distributional characteristics of many insect populations (Hassell 1978), which are the key resources of insect parasites. Locality learning may, therefore, be a potentially adaptive trait for many insect parasites.

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