

# Behaviorally mediated spatial and temporal refuges from a cleptoparasite, *Argochrysis armilla* (Hymenoptera: Chrysididae), attacking a ground-nesting wasp, *Ammophila dysmica* (Hymenoptera: Sphecidae)

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**Summary.** It has been suggested that parasite pressure favors the evolution of sociality within the Hymenoptera. I analyzed the impact of a chrysidid nest parasite, *Argochrysis armilla*, on its host, the solitary ground-nesting wasp, *Ammophila dysmica*, to assess the role of parasitism in favoring two steps towards sociality: aggregated nesting and delayed nest provisioning. The foraging strategy of *Argochrysis armilla* involves discovering host nests during excavation, learning the locations of discovered nests, and returning to oviposit in nests during nest provisioning; I therefore assessed the influence of host behavior on (1) parasite discovery of nests and (2) parasite oviposition in nests. Significantly fewer parasites discovered host nests that were excavated during the early morning and late afternoon, due to partial asynchrony of host and parasite activity. Nests excavated in areas of low nest density were also less likely to be discovered; use of low density nest sites increased during periods of high parasite activity. Due to a rapidly decelerating rate of parasite recruitment to nests under excavation, the duration of nest digging had only a limited influence on nest discovery by parasites. The probability of parasite oviposition in a host nest was determined by the number of parasites discovering the nest during excavation and by the time between nest excavation and provisioning; delaying nest provisioning reduced the risk of parasite oviposition. Delayed provisionings primarily appeared to be a result of the stochastic process of hunting and prey encounter. The number of provisions placed in a nest (one vs two) had no effect on the probability of nest parasitism. Spatial patterns of parasitism were directly density depen-

dent in 1984 and density independent in 1986. In this system parasite pressure acts against the formation of nesting aggregations and in favor of delayed nest provisioning. The dependence of these results on species-specific aspects of the parasite's foraging strategy and the host's defensive strategy suggests, however, that different parasite species may generate qualitatively different selection pressures, potentially contributing to the diversity of nesting behavior in the Hymenoptera.

## Introduction

Eusociality has evolved many times in the Hymenoptera, apparently through at least two series of evolutionary steps, the subsocial and semisocial pathways (Michener 1958, 1969, 1985; Brockmann 1984; Nonacs 1988). The subsocial pathway envisions the origin of social behavior in groups consisting of single mothers and their offspring, whereas the semisocial pathway envisions sociality arising in groups of variously related adult females. Although these pathways are quite different, selective pressures exerted by parasites and predators have been postulated to be important forces driving evolution along both routes (Andersson 1984). Mutualism related to nest defense and a general kin selection model may explain the entire transition from solitary to eusocial behavior via semisociality (Lin 1964; Michener 1969; Wilson 1971; Lin and Michener 1972; West-Eberhard 1978; Rasnitsyn 1980; Rissing et al. 1989). Although parental manipulation (Alexander 1974) or haplodiploidy coupled with kin selection are generally used to explain the evolution of sterile workers via subsociality (Hamilton 1964; Godfray and Grafen 1988), natural enemy pressures are still invoked

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to explain earlier evolutionary steps towards sociality (Michener 1969; Wilson 1971; Evans 1977; Rasnitsyn 1980). The importance of natural enemies in the evolution of social traits has been supported by empirical studies demonstrating improved nest defense against conspecific nest-usurping “parasites” in facultatively semisocial wasps (e.g., Gamboa 1978; Klahn 1988) and facultatively communal bees (Velthuis 1987; Gerling et al. 1989). Grouping may also facilitate recovery from nest predation by vertebrates (Strassman et al. 1988). However, relatively few studies have been directed at understanding the importance of interspecific parasitism in shaping the earliest expressions of social behavior (e.g., Sakagami and Maeta 1977).

In this paper, I assess the influence of a nest parasite on the costs and benefits of two host traits that may be important to the evolution of sociality: aggregated nesting and delayed nest provisioning. Aggregated nesting facilitates interactions between nesting females, including nest sharing, and as such represents an important initial step towards sociality via the semisocial route. The delay of nest provisioning until after the egg hatches effects a shift from a “solitary” lifestyle, with no mother-offspring contact, to a “subsocial” lifestyle, incorporating interactions between the mother and the developing larva (Wilson 1971). Delayed nest provisioning therefore represents an initial step along the subsocial route to sociality.

Aggregated nesting may be favored if it confers improved protection from predators or parasites (Alexander 1974; Rosenheim 1990). Some authors support the notion of a refuge from natural enemies in areas of high nest density, i.e., inversely density-dependent mortality (Alcock 1974; Rubink 1978; Endo 1980; Hager and Kurczewski 1985; Willmer 1985a; Gamboa et al. 1986; Evans and O’Neill 1988), while others support the reverse pattern of directly density-dependent mortality (Lin 1964; Lin and Michener 1972; Brockmann 1979, 1984; Rasnitsyn 1980). Empirical studies of spatial density-dependence of host mortality have also yielded mixed results (reviewed by Rosenheim 1990); these studies have generally been conducted without a knowledge of the foraging strategy of the natural enemy or the defensive strategies of the host.

Delayed nest provisioning has been suggested to function both as a means of providing the developing larva with fresh, and therefore high quality, provisions (Malyshev 1968) and as a potential defense against parasitic flies (Diptera: Sarcophagidae) (Evans 1957). Hager and Kurczewski (1985)

demonstrated that larvae deposited in host nests by fly parasites were able to exploit host nests effectively only if they contained a host egg. Thus, by delaying nest provisionings and the associated risk of parasitic fly attack until after egg hatch, host wasps appeared to reduce nest parasitism.

Here I examine ecological and behavioral factors that modulate the impact of a cleptoparasite, *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), on its host, *Ammophila dysmica* Menke (Hymenoptera: Sphecidae), in an attempt to elucidate potential selective forces on host behavior. I address factors that influence (1) the probability of nest discovery by *Argochrysis armilla* and (2) the ability of parasites to oviposit successfully in discovered host nests.

## Methods

### Natural history

Interactions of *Ammophila dysmica* and *Argochrysis armilla* were studied 1982–1988 at Sagehen Creek Field Station, Nevada County, California, USA (Rosenheim 1987a). The study site was located on a broad ridgetop, elevation 2000 m, where *Ammophila dysmica* nested both as scattered individuals and in aggregations located along a dirt road. *Ammophila dysmica* requires an average of 61.9 min (SD = 32.2,  $n = 114$ ) to excavate shallow, unicellular nests. Nests are excavated and temporarily sealed prior to hunting for provisions, which consist of one or (in approximately 25% of all nests) two lepidopteran larvae. Nests are most vulnerable to parasitism by *Argochrysis armilla* when the host has opened the nest to add provisions and oviposit (average duration: 181.2 s, SD = 119.6,  $n = 61$ ). The single host egg is deposited when the first provision is placed in the nest. Eggs hatch in 2 days. Mother-offspring contact will therefore occur if a second provision is added  $\geq 2$  days after the first. *Ammophila dysmica* completes the nesting cycle before digging the next nest.

*Argochrysis armilla* is the dominant mortality factor acting on *Ammophila dysmica*, achieving annual parasitism rates of 21.3–43.5%. Other natural enemies individually cause mean annual mortalities of  $\leq 2.9\%$  (Rosenheim 1987a). *Argochrysis armilla* locates nests through visual attraction to nest-digging host wasps. Nests being excavated are, however, not vulnerable to parasitism. Parasites learn the locations of discovered nests and subsequently monitor active nests during the host’s absence, waiting for an opportunity to enter the nest and oviposit when the host provisions (Rosenheim 1987b). Fully provisioned nests receive extensive final closures that are impervious to *Argochrysis armilla*.

### Nest discovery

Factors influencing the discovery of host nests during excavation were investigated during 1986 (22 June–21 July). Two independent measures of the number of *Argochrysis armilla* discovering a nest were used. First, the abundance of parasites during nest digging was measured as the maximum number of parasites simultaneously attending the nest at any time during the entire excavation. This measure estimates the minimum number of parasites locating a nest. Parasites were defined to be in attendance if they landed at, or hovered directly over, the nest en-

trance, or if they perched twice sequentially during the sampling period orienting towards the nest from within 30 cm. Second, the number of parasites discovering a nest was inferred from the number of parasites monitoring the nest during the host's absence. This inferred measure is based upon the finding that only parasites that discover a nest during its excavation, and therefore have an opportunity to learn its location, are subsequently able to monitor the nest during the host's absence (Rosenheim 1987b). Three-minute surveys of nests were performed hourly during the period of high parasite activity, 1100–1600 h, for 5 days after nest excavation or 1 day after final provisioning. Parasite abundance was scored as the maximum number of parasites simultaneously attending the nest during the 3-min sample. A mean abundance score was obtained by averaging survey scores over the 2 days following nest construction.

I assessed the roles of four factors in determining nest discovery by *Argochrysis armilla*: (1) daily cycles of *Argochrysis armilla* activity, (2) seasonal effects, (3) duration of nest digging, and (4) local *Ammophila dysmica* nest density. Daily cycles of parasite activity were quantified by averaging for each hour of nesting activity, 0900–1800 h, results of the previously described 3-min surveys of nest-monitoring parasite abundance. The mean hourly parasite activity level for the hour during which a nest was excavated was assigned to that nest as a measure of parasite activity. Nest excavations frequently overlapped more than one hourly interval; in these cases the largest mean hourly parasite activity level for an hour during which nest excavation occurred was chosen as an index of parasite activity. Seasonal effects were investigated by assigning a season date (22 June = day 1, 21 July = day 30) to each nest's day of excavation. The duration of nest digging activity was measured directly as the time between the beginning of nest excavation and the completion of the temporary closure, with interruptions of  $\geq 10$  min subtracted from the total. Local density of *Ammophila dysmica* nests was measured as the proportion of all previously excavated *Ammophila dysmica* nests that were constructed within a 2 m radius of the nest in question. In 1986 the locations of other *Ammophila* spp. nests were not recorded, which likely incorporated some error into density measurements. The selection of a 2 m radius was based upon an analysis of *Argochrysis armilla* foraging designed to reveal the dimensions of the parasite-perceived host "patch" (Rosenheim et al. 1989).

#### Oviposition in host nests

Factors influencing the probability of *Argochrysis armilla* oviposition in host nests were investigated in 1984 (30 June–21 August) and 1986 (22 June–21 July). During the 1984 field season a large study area (0.125 km<sup>2</sup>) was censused daily to assess the importance of local nest density. The locations of all nesting *Ammophila* spp. were recorded, including nests of the preferred host of *Argochrysis armilla*, *Ammophila dysmica* ( $n=82$ ), a less preferred host *Ammophila azteca* Cameron ( $n=197$ ), and a rarely exploited host *Ammophila marshi* Menke ( $n=36$ ). Although census time was distributed approximately evenly across the site, only a minority of all nests constructed were discovered, so density estimates are meaningful only as relative measures. Density was measured as the total number of *Ammophila* spp. nests constructed at any time during the field season within a 2 m radius of the nest in question. Parasite oviposition in nests was assessed by excavating nests at season's end and searching for parasite or host cocoons.

During 1986 a smaller study site (250 m<sup>2</sup>) was observed intensively to assess the importance of behavioral factors as well as nest density. Oviposition by *Argochrysis armilla* was determined both by direct observations of parasite penetration of nests during provisioning, which was consistently associated

with parasite oviposition, and by nest excavations at season's end. The number of individual parasites successfully penetrating nests was also recorded. The roles of six factors were investigated: (1) parasite abundance during nest digging, (2) daily cycles of parasite activity, (3) seasonal effects, (4) number of lepidopteran larvae provisioned, (5) time between nest digging and nest provisioning, and (6) local nest density. Parasite abundance during nest digging and local density of *Ammophila dysmica* nests were measured as just described under "Nest discovery." Hourly parasite activity and seasonal effects were investigated as before, except that values now reflected the timing of nest provisioning rather than nest digging; values represent an average of two figures for nests receiving two provisions. The number of provisions, one or two, was determined from direct observations of provisioning activity and from the recovery of head capsules from nest cells during nest excavations. The time between nest digging and nest provisioning was calculated by including only time elapsed during the daily 9.5 h of *Ammophila dysmica* activity (0900–1830 h); times were averaged for nests receiving two provisions.

To determine if *Ammophila dysmica* modulated its hunting activity to affect the timing of nest provisioning, the distribution of hunting times (i.e., the time between nest digging and nest provisioning or between successive provisionings) was compared to an exponentially decaying distribution, which would be expected under the assumptions of (1) constant hunting activity and (2) a fixed probability of prey capture per unit hunting time. Decay rates for expected distributions were obtained as the slope of the linear regressions of  $[\ln(\text{the total number of wasps still hunting} + 0.5)]$  on the time since the initiation of hunting. Observed and expected distributions were compared with the Kolmogorov-Smirnov test for goodness of fit.

Minor mortality factors (the cleptoparasitic fly *Hilarella hilarella* Zedterstedt [Diptera: Sarcophagidae], uncharacterized elements leading to the death and molding of cell contents before cocoon spinning, and cells whose contents were discarded by intruding conspecific wasps or the resident host wasp, in the latter case apparently in response to the detection of nest parasites were recorded in relation to nest density to assess their influence on the costs and benefits of aggregated nesting.

#### Statistical analysis

Factors influencing nest discovery by *Argochrysis armilla* were analyzed with stepwise multiple regression; when mean parasite abundance during 3-min surveys was used as the dependent variable, observations were weighted by the number of surveys performed. A stepwise logistic regression was used to analyze influences on parasite oviposition and accommodate the binary dependent variable (i.e., the nest was, or was not, subject to parasite oviposition). Test probabilities reported for the stepwise multiple and logistic regressions are 1-tailed for those variables where previous work had indicated alternate hypotheses to the null hypothesis; these variables were (1) parasite abundance during nest digging, (2) hourly parasite activity levels, (3) the duration of nest digging, (4) the number of provisions, (5) the time between nest digging and nest provisioning, and (6) local nest density. All other probability values are for 2-tailed tests. Analyses were performed with the BMDP computer statistical package (Dixon 1985).

## Results

### Nest discovery

Host nest discovery by *Argochrysis armilla*, measured either as parasite attendance of nests during

**Table 1a.** Multiple regression analysis of factors influencing the attendance of *Ammophila dysmica* nests by the parasite *Argochrysis armilla* during nest excavation

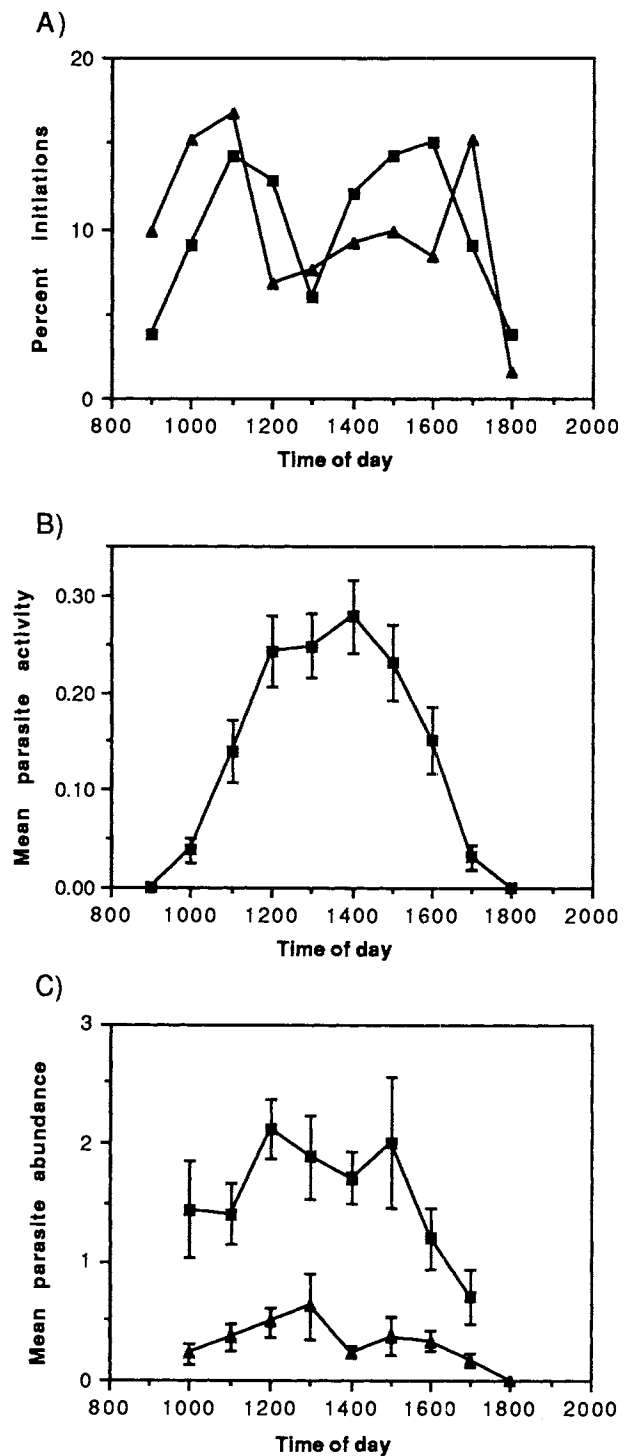
Independent variable ( <i>df</i> )	Regression coefficient	<i>P</i>	Partial correlation coefficient ( <i>r</i> )	Total <i>r</i>
a) Hourly parasite activity (105)	5.563	<0.001	0.424	–
b) Local nest density (105)	5.199	<0.001	0.384	–
c) Digging duration (102)	0.001	0.34	–	–
d) Season date (102)	–0.006	0.87	–	–
Total model (a + b) ( <i>df</i> = 105)	–	<0.001	–	0.480

**Table 1b.** Multiple regression analysis of factors influencing the monitoring of *Ammophila dysmica* nests by the parasite *Argochrysis armilla* during the host's absence

Independent variables ( <i>df</i> )	Regression coefficient	<i>P</i>	Partial correlation coefficient ( <i>r</i> )	Total <i>r</i>
a) Hourly parasite activity (111)	1.677	<0.001	0.337	–
b) Local nest density (111)	2.323	<0.001	0.431	–
c) Digging duration (106)	–0.002	0.19	–	–
d) Season date (106)	0.001	0.88	–	–
Total model (a + b) ( <i>df</i> = 111)	–	<0.001	–	0.462

excavation or parasite monitoring of nests during the host's absence, was significantly influenced by daily cycles of parasite activity and local nest density but not by the duration of nest digging or season date (Table 1a, b).

Hourly variation in foraging activity of *Argochrysis armilla* appeared to create a temporal refuge from parasite detection for *Ammophila dysmica* (Fig. 1a, b, c). Parasite activity, as measured by hourly censuses of nest-attending parasites, showed a single broad peak at midday (1200–1500 h) and was low or absent in the early morning and late afternoon. In contrast, host activity was bimodal, with peaks in the midmorning (1000–1200 h) and mid to late afternoon (1500–1700 h) and spanned a longer portion of the day (Fig. 1a, b; Rosenheim 1987a). This asynchrony between parasite and host reduced the probabil-



**Fig. 1.** Daily activity patterns of *Ammophila dysmica* and its nest parasite, *Argochrysis armilla*. (A) Percent nest excavations (triangles;  $n=132$ ) and provisionings (squares;  $n=133$ ) initiated by *Ammophila dysmica* during 1-h periods, 0900–1800 h. (B) Mean ( $\pm$  SE) hourly parasite activity, as measured by 3-min surveys ( $n_{tot}=2005$ ) of nest-attending parasites. (C) Influence of the hour of nest excavation on the number of parasites discovering host nests under excavation, as measured by the abundance ( $\bar{x} \pm$  SE) of parasites attending nests during excavation (squares;  $n_{tot}=105$ ) and during the host's absence (triangles;  $n_{tot}=111$ ).



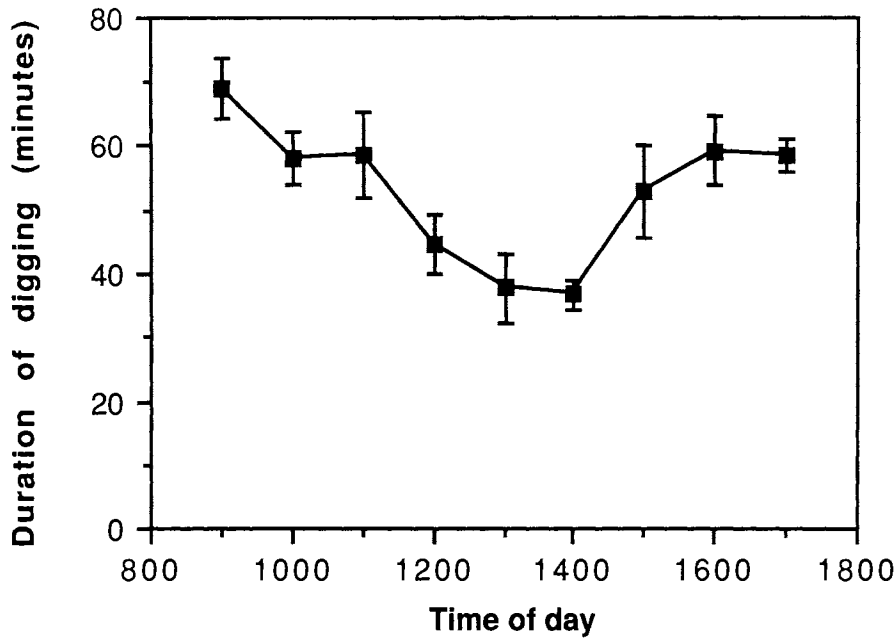


Fig. 2. Hourly variation in the mean ( $\pm$ SE) duration of nest digging by *Ammophila dysmica*, 1986 ( $n=108$ ).

ity of parasites discovering nests excavated in the early morning or late afternoon (Fig. 1c). One factor partly restricting the ability of *Ammophila dysmica* to exploit this temporal refuge was the longer time required to excavate nests during the early morning and late afternoon (Fig. 2). Longer nest excavation times made it less likely that excavations could be initiated and completed during a window of low parasite activity.

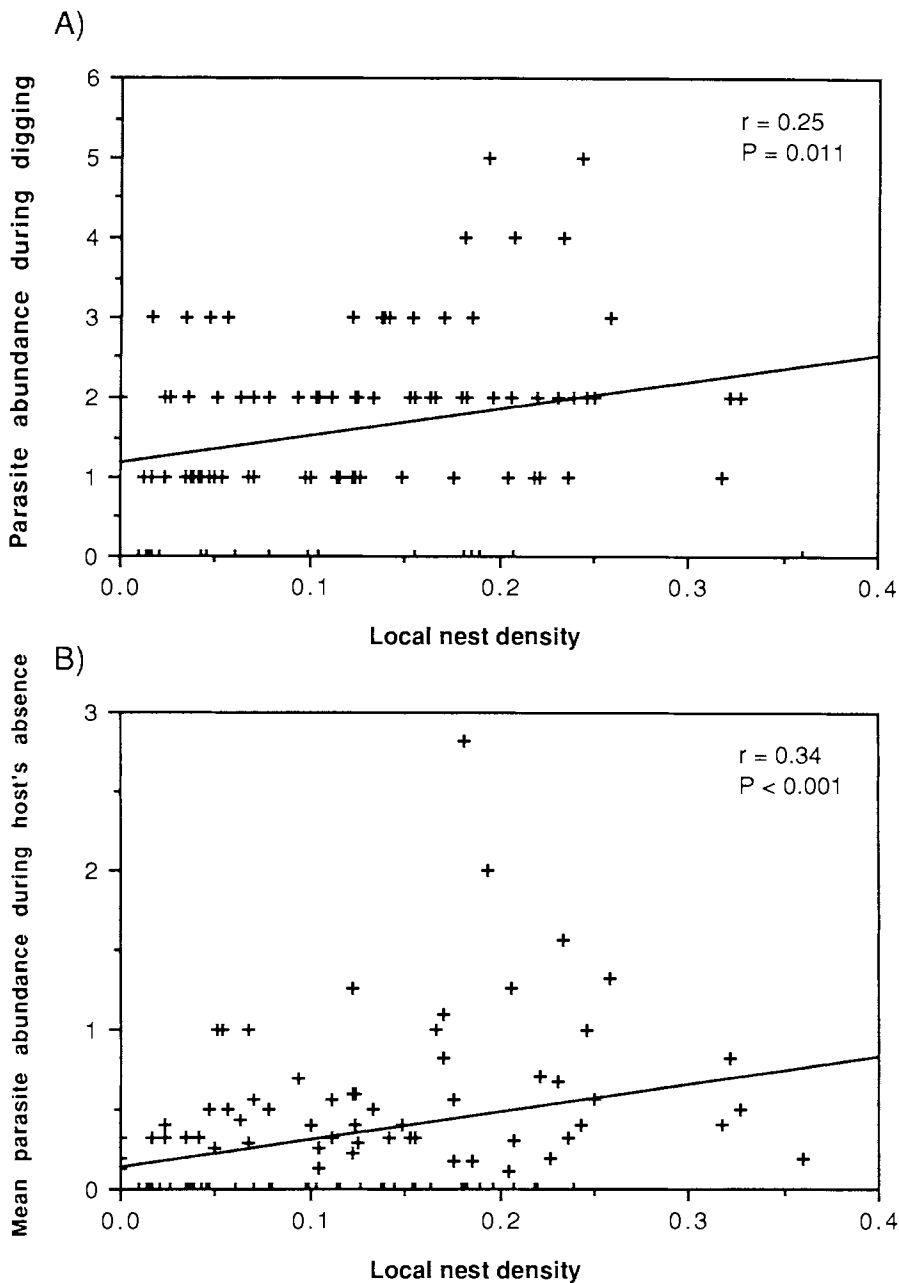
Directly density-dependent foraging by *Argochrysis armilla* appeared to create a partial refuge from parasite detection in areas of low nest density (Fig. 3a, b). This was evident in both the attendance of nests being excavated and the subsequent monitoring of nests during the host's absence. The significant negative correlation between local nest density and hourly levels of parasite activity (Table 2) indicates that the use of low-density nest sites predominated during periods of high parasite activity. Thus, spatial and temporal refuges appeared to function partly as complementary or alternative tactics of parasite avoidance.

The failure of the duration of nest digging to significantly influence nest discovery by *Argochrysis armilla* (Table 1a, b) was somewhat counterintuitive, since one would expect longer nest excavations to have a greater overall apparency to foraging parasites that are attracted to nest-digging hosts (Rosenheim 1987b). An inspection of the time course of parasite recruitment to nests under excavation reveals, however, a rapid recruitment of parasites during the first 17 min of nest excavation, followed by a strongly decelerating rate of

recruitment (Fig. 4), apparently reflecting the existence of relatively complete spatial or temporal refuges from parasites. The fraction of nests discovered by one or more parasites increased only from 65.7% to 78.1% between 22 and 130 min after the start of digging activity, the shortest and longest nest excavation times observed, respectively. Due to my inability to distinguish individual parasites, I was unable to measure directly the change in the total number of parasites that located a nest as digging proceeded. However, the results of the multiple regression analyses (Table 1a, b) and the data in Figure 4 suggest that variation in digging time has only limited influence on nest discovery by *Argochrysis armilla*. This result was further confirmed by repeating the multiple regression analysis with the duration of nest digging measured as a fraction of the mean hourly digging duration (Fig. 2) to remove hourly trends; the new variable again failed to make a significant contribution to the regression equation (regression coefficient =  $-0.1169$ , SE =  $0.1262$ ,  $t = -0.93$ ,  $df = 104$ ,  $P = 0.18$ ).

#### Oviposition in host nests

The stepwise logistic regression revealed two significant influences on the probability that an *Argochrysis armilla* would oviposit in a host nest during 1986: (1) the number of parasites discovering the nest during excavation and (2) the time between nest digging and nest provisioning (Tables 3, 4; see also Rosenheim 1988). Variables not making



**Fig. 3.** Directly density-dependent foraging by the nest parasite *Argochrysis armilla*. Abundance of nest-attending parasites (A) during nest excavation (slope = 3.35, SE = 1.29,  $n = 105$ ), and (B) during the host's absence (slope = 1.73, SE = 0.47,  $n = 111$ ) plotted against local nest density

significant contributions were (i) hourly levels of parasite activity, (ii) season date, and (iii) number of provisions; local nest density was marginally significant (Tables 3, 4).

The time between nest excavation and nest provisioning appeared to act as a partial barrier to nest exploitation by *Argochrysis armilla* (Fig. 5). During the host's absence from the nest while hunting for provisions, parasite monitoring of nests declined gradually over a period of days. This decline paralleled the decreasing proportion of eventually-provisioned nests that remained uncompleted. The shrinking pool of nest-attending para-

sites resulted in an increasing probability of escape from parasite oviposition, especially evident for nests provisioned more than 1100 min after nest construction (Fig. 5b). The analysis is strengthened if parasite oviposition is analyzed on a per-provisioning basis rather than a per-nest basis (thereby treating independently each provisioning of doubly provisioned nests). The mean time between nest excavation and nest provisioning was significantly greater for provisionings escaping parasite oviposition than for those subject to parasite oviposition (Table 4).

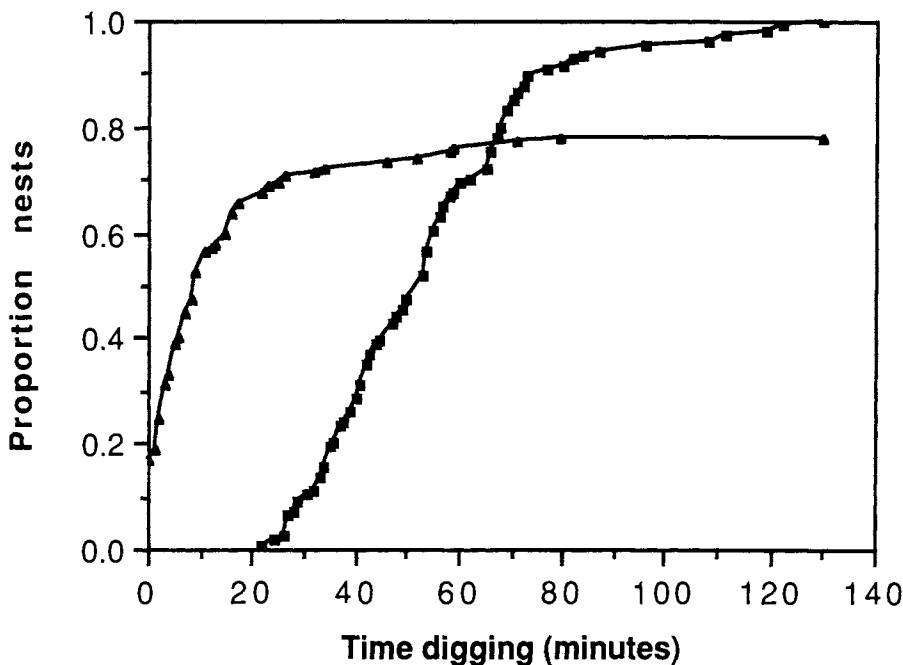
The distribution of *Ammophila dysmica* hunt-

**Table 2.** Correlation matrix of factors influencing the discovery of *Ammophila dysmica* nests by the parasite *Argochrysis armilla*. Parasites digging, the number of parasites discovering the nest during digging; Parasites monitoring, the number of parasites monitoring the nest during the host's absence

	Parasites digging	Hourly parasite activity	Local nest density	Digging duration	Season date
Parasites digging	–				
Hourly parasite activity	0.292**	–			
Local nest density	0.245*	–0.334***	–		
Digging duration	–0.062	–0.224*	0.046	–	
Season date	–0.080	0.122	–0.246*	–0.011	–
Parasites monitoring	0.574***	0.189	0.349***	–0.147	–0.041

First five rows  $df=102$ , bottom row  $df=103$  for the first variable, 106 thereafter

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$



**Fig. 4.** Time course of recruitment of the nest parasite *Argochrysis armilla* to host nests ( $n=108$ ) during nest excavation. Squares, cumulative percent of nest excavations completed; triangles, cumulative percent of nests discovered by one or more parasites. The cumulative percent nests discovered by parasites was calculated using the total sample ( $n=108$ ) for the entire 0–130 min period; nests completed before 130 minutes were therefore fixed as either discovered or not discovered for the remaining time plotted

**Table 3.** Stepwise logistic regression analysis of factors influencing the probability of oviposition by the parasite *Argochrysis armilla* into nests ( $n=75$ ) of *Ammophila dysmica*. Parasites digging, the number of parasites discovering the nest during digging; Time barrier, the time between nest excavation and nest provisioning

Step number	Variable entered	Log likelihood	Improvement chi-square	$P$
1	Parasites digging	–42.702	13.702	<0.001
2	Time barrier	–40.818	3.767	0.026
	Variables not entered		Approximate F to enter	$P$
	Hourly parasite activity		0.30	0.292
	Local nest density		2.51	0.059
	Season date		1.15	0.286
	Number of provisions		0.68	0.206

ing times deviated significantly from an exponentially decaying distribution in 1986 ( $D=0.185$ ,  $df=111$ ,  $P < 0.01$ ) and 1988 ( $D=0.240$ ,  $df=22$ ,  $P < 0.01$ ) but not in 1983 ( $D=0.211$ ,  $df=8$ ,  $P > 0.20$ ). A slight trend towards delayed provisioning was apparent in both 1986 and 1988 (Fig. 6); the observed delays were significant between 62 and 909 min for the 1986 distribution and between 198 and 346 min for the 1988 distribution. Thus one or both of the assumptions regarding *Ammophila dysmica* hunting behavior (i.e., [1] constant hunting activity and [2] a fixed probability of prey capture per unit hunting time) appears to be violated. Despite hourly variation in nest provisioning activity during 1986 (Fig. 1a), the hour of hunt initiation did not have a significant effect on hunt duration (ANOVA:  $F=1.29$ ,  $df=9$ ,  $P=0.25$ ).

Despite the fact that doubly provisioned nests

**Table 4a.** Summary statistics for oviposition by the parasite *Argochrysis armilla* into nests of *Ammophila dysmica* during nest provisioning, analyzed on a per-nest basis

	Number of nests yielding <i>Argochrysis armilla</i> cocoons (%)	Number of nests destroyed by other mortality factors <sup>a</sup> (%)	Parasite abundance during nest digging			Local nest density			Number of provisions		
			$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>
Nests subject to oviposition during nest provisioning ( <i>n</i> = 45)	37 (82.2%)	8 (17.8%)	2.13	0.98	32	0.133	0.095	41	1.200	0.405	45
			***			*			NS		
Nests escaping oviposition during nest provisioning ( <i>n</i> = 82)	4 (4.9%)	5 (6.1%)	1.23	1.04	52	0.097	0.078	72	1.231	0.424	78

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$

<sup>a</sup> Including nests destroyed by the parasitic fly *H. hilarella*, nests containing fungi, nests whose contents were discarded by female *Ammophila dysmica*, and a nest containing an uneaten caterpillar. The categorization of nests as subject to oviposition or not is based upon direct observations of nest provisionings as well as nest excavations. These figures underestimate the impact of minor mortality factors, because nests for which provisionings were not observed in entirety could not be classified as subject to oviposition or not, and therefore were omitted. For more accurate estimates of minor mortality factor impact, see Rosenheim (1987a)

**Table 4b.** Summary statistics for oviposition by the parasite *Argochrysis armilla* into the nests of *Ammophila dysmica* during nest provisioning, analyzed on a per-provisioning basis. Time barrier, time between nest excavation and nest provisioning

	Time barrier (min)			Hourly parasite activity			Season date		
	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>
Provisionings subject to oviposition	499.8	423.8	31	0.172	0.087	36	12.27	8.45	38
	**			NS			NS		
Provisionings escaping oviposition	835.9	645.5	66	0.161	0.095	79	14.63	7.68	78

NS:  $P > 0.1$ ; \*\*  $P < 0.01$

present repeated opportunities for *Argochrysis armilla* oviposition, increased oviposition into these nests was not observed during 1986 (Tables 3, 4). Similarly, the observed probability of nest parasitism during 1983 and 1984 was independent of the number of provisions (singly provisioned nests, 18 of 46 parasitized; doubly provisioned nests, 7 of 15 parasitized;  $G = 0.264$ ,  $P > 0.5$ ).

Although local nest density exerted only a marginally significant *direct* effect on the probability of parasite oviposition (Table 3), nests subject to *Argochrysis armilla* oviposition were found in areas of significantly higher local nest density than those escaping parasite oviposition (Table 4). This result is apparently mediated by local nest density operating indirectly on parasite oviposition through its effect on parasite discovery of nests under excavation. The number of *Argochrysis armilla* penetrating nests during provisioning was also significantly correlated with local nest density (Fig. 7).

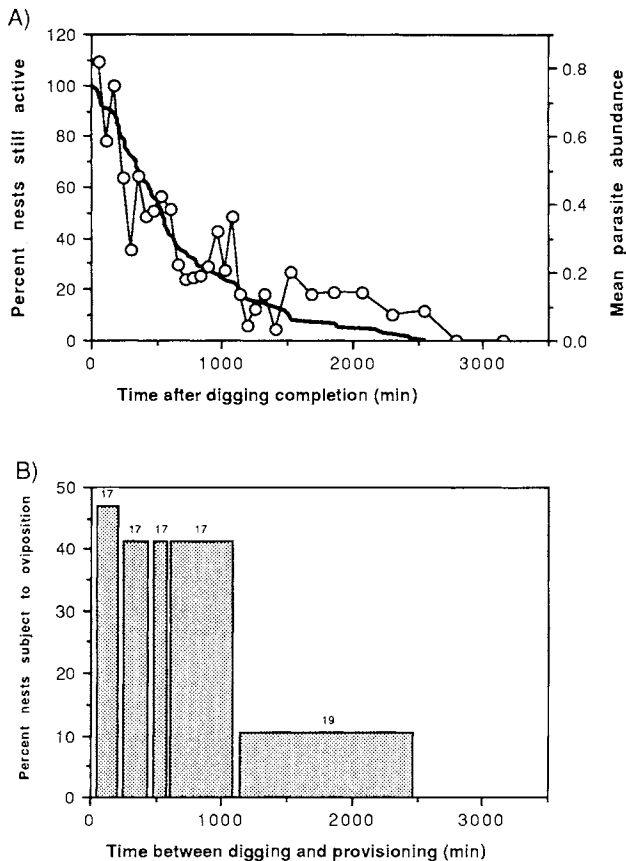
#### Density-dependent nest mortality

Despite these patterns of density-dependent oviposition by *Argochrysis armilla*, the distribution of

nests yielding parasite cocoons at the end of the season was density independent (mean local density for nests producing *Argochrysis armilla* = 0.1203, SD = 0.0994,  $n = 33$ ; for nests producing *Ammophila dysmica* = 0.0967, SD = 0.0785;  $t = -1.30$ ,  $df = 100$ ,  $P > 0.10$ ). *Argochrysis armilla* developmental success was affected by other parasites, predators, pathogens, and the tendency of the host wasp to destroy parasitized nests by discarding cell contents (Table 4; see also Rosenheim 1987a). These diverse mortality factors appeared to generate enough random variation to mask the underlying density-dependent action of *Argochrysis armilla*. Nest parasitism was, however, directly density-dependent during the 1984 season (mean local density for nests producing *Argochrysis armilla* = 23.00, SD = 9.80,  $n = 17$ ; for nests producing *Ammophila dysmica* = 16.03, SD = 11.48,  $n = 38$ ;  $t = 2.12$ ,  $df = 53$ ,  $P < 0.05$ ).

Nest mortality induced by agents other than *Argochrysis armilla* was independent of local nest density in 1986. Mean local nest density for 3 nests destroyed by the parasitic fly *H. hilarella*, 17 nests with fungi developing on cell contents, 3 nests whose contents were discarded by female *Ammo-*





**Fig. 5.** Effect of the timing of nest provisioning by *Ammophila dysmica* on the abundance of nest-monitoring parasites, *Argochrysis armilla*, and the associated risk of parasite oviposition during provisioning. (A) Solid line, percent of eventually-provisioned nests ( $n=111$ ) remaining uncompleted. Open circles, mean abundance of nest-monitoring parasites as measured during 3-min nest surveys ( $n_{\text{tot}}=943$ ). (B) Percent nests subject to oviposition, calculated by grouping completed nests approximately evenly into five categories: those with mean times between nest digging and provisioning of 19–217 min, 219–449 min, 450–589 min, 590–1094 min, and 1121–2445 min. Numbers above histogram bars are the number of nests in the sample

*phila dysmica*, and one nest containing an uneaten caterpillar ( $\bar{x}=0.1202$ ,  $SD=0.0732$ ,  $n=24$ ) was not significantly different from that of nests yielding *Ammophila dysmica* cocoons ( $t=1.28$ ,  $df=91$ ,  $P>0.20$ ). Total nest mortality due to the combined action of *Argochrysis armilla* and all minor mortality factors was also density independent (mean local density for destroyed nests = 0.1203,  $SD=0.0886$ ,  $n=57$ ;  $t=1.41$ ,  $df=124$ ,  $P>0.10$ ).

The collective impact of mortality factors other than *Argochrysis armilla* was *inversely* density dependent during 1984, suggesting a potential balancing force to the directly density-dependent action of *Argochrysis armilla*. Mean local nest density for two nests destroyed by *H. hilarella*, one nest containing only a single unidentified Diptera pu-

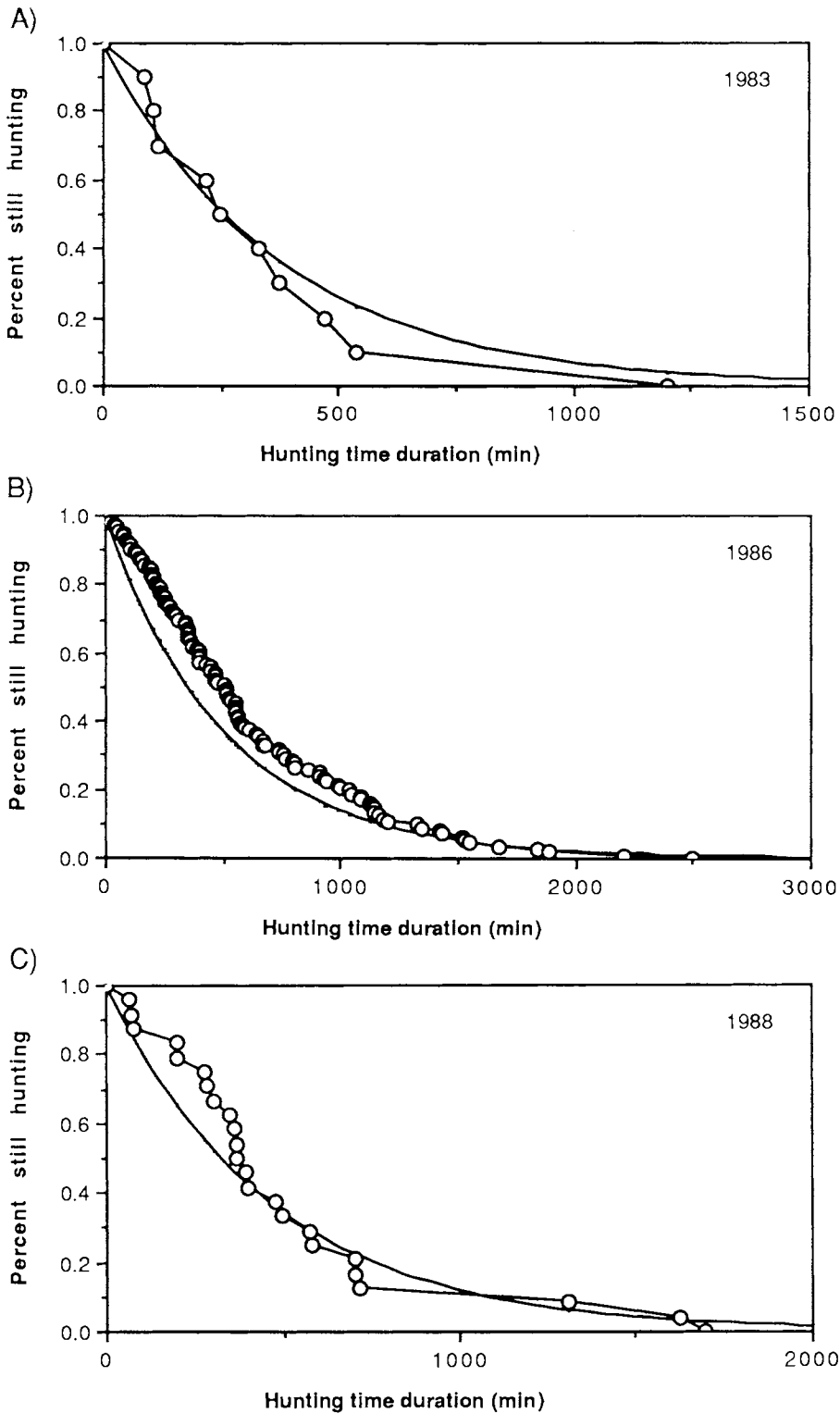
parium, seven nests with fungi developing on cell contents, and one nest destroyed by a raiding female *Ammophila dysmica* ( $\bar{x}=9.64$ ,  $SD=8.04$ ,  $n=11$ ), was significantly lower than that of nests yielding *Ammophila dysmica* cocoons ( $t=2.07$ ,  $df=47$ ,  $P<0.05$ ). As in 1986, total nest mortality due to the combined impact of *Argochrysis armilla* and all minor mortality factors was density independent (mean local nest density for destroyed nests = 17.75,  $SD=11.18$ ,  $n=28$ ;  $t=-0.60$ ,  $df=64$ ,  $P>0.5$ ).

## Discussion

The ability of *Argochrysis armilla* to exploit nests of *Ammophila dysmica* appears to be determined in large part by specific aspects of host behavior. Two factors influenced the ability of parasites to discover nests under excavation: (1) the timing of digging activity and (2) local nest density. These factors defined two refuges from parasite detection: first, a temporal refuge during the early morning and late afternoon and second, a spatial refuge in areas of low nest density. These refuges appeared to operate complementarily; nest sites were selected in areas of relatively low nest density during hours of relatively high parasite activity. A possible mechanism contributing to this complementarity is the ability of *Ammophila dysmica* to evaluate the local abundance of natural enemies during the initial stages of nest excavation, coupled with the propensity of digging wasps to abandon nest sites attended by large numbers of parasites (Rosenheim 1988). *Ammophila dysmica* may thus be discouraged from initiating nests in high density areas due to the concentration of foraging *Argochrysis armilla* present there during the midday hours.

Two additional factors were key influences on the probability that a host nest would be oviposited in by *Argochrysis armilla*: (1) the number of parasites discovering the nest during excavation and (2) the length of time between nest excavation and provisioning. The discovery of host nests during nest excavation is central to the foraging strategy of *Argochrysis armilla*, which is based upon a learned knowledge of host nest locations (Rosenheim 1987b). In delaying nest provisioning, host wasps appeared to acquire a second kind of temporal refuge from parasites by increasing the time between the phase of the nesting cycle that is conspicuous to parasites (i.e., nest digging) and the phase of the nesting cycle that is vulnerable to parasites (i.e., nest provisioning).

Although local nest density did not have a strong *direct* effect on oviposition by *Argochrysis*



**Fig. 6.** Distributions of hunting time durations of *Ammophila dysmica*. Solid line, distribution expected under the assumptions of constant hunting activity and a fixed probability of prey capture per unit hunting time; decay rate parameters for the expected distributions were obtained from observed hunting time distributions. Open circles, observed distributions. (A) 1983 (B) 1986 (C) 1988

*armilla*, parasite oviposition was more likely in areas of high nest density. Nest parasitism, measured as the successful development of *Argochrysis armilla* in host nests, was also more likely in areas of high nest density, at least during 1984. Local

nest density appeared to influence nest exploitation indirectly via its effect on the probability of nest discovery. Other sources of nest mortality were density independent in 1986 and inversely density dependent in 1984. The larger 1984 study site in-

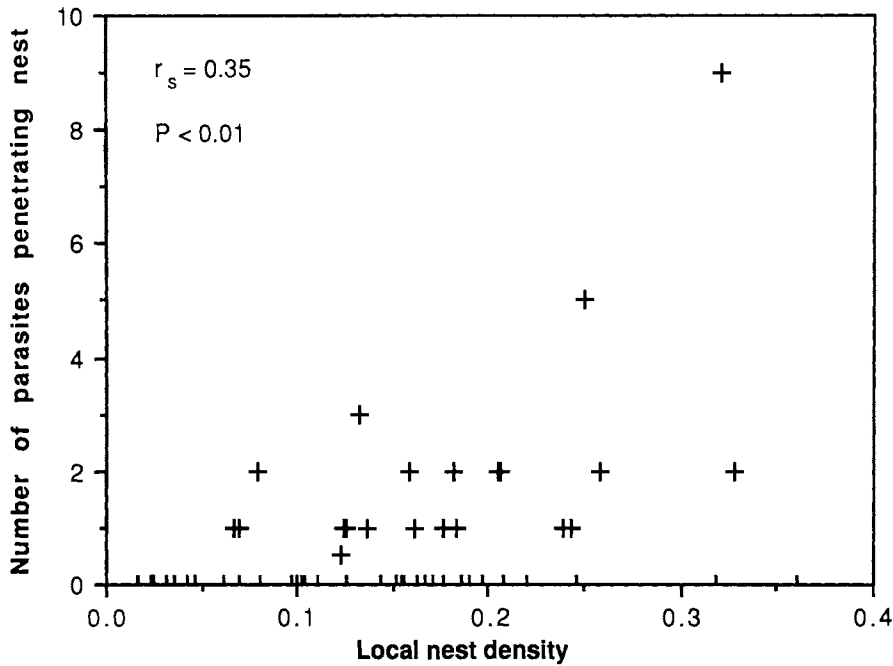


Fig. 7. Effect of local *Ammophila dysmica* nest density on the number of parasites, *Argochrysis armilla*, penetrating the nest during provisionings ( $n = 59$ )

cluded a greater diversity of nesting areas and presumably an increased range of substrate conditions. Despite the small sample size, the data from 1984 suggest that nest-site selection by *Ammophila dysmica* may have evolved under balancing selection since *Argochrysis armilla* favored dispersed nesting and a combination of minor mortality factors favored aggregated nesting. The death and molding of cell contents in predominantly low density areas suggests that these areas may be less suitable for wasp development. Additional work is needed to identify key environmental conditions affecting immature development success and overwintering survival.

Thus, three aspects of *Ammophila dysmica* behavior appear to significantly reduce parasite impact: dispersed nesting, activity during the early morning and late afternoon, and delayed provisioning. Of these, at least the latter two probably do not represent adaptations of *Ammophila dysmica* to avoid parasitism. Rather, they are likely to be side-effects of other processes (thermal constraints and stochastic prey searching, respectively), as discussed below. The observation that these behaviors result in reduced parasite impact does, however, provide an insight into the evolutionary consequences of these behavioral traits in other species subject to similar selection pressures.

#### *Asynchrony of host and parasite*

Within-day asynchrony of host and parasite has been hypothesized to influence patterns of nest

parasitism by a complex of parasitic flies (Evans et al. 1980) and has been demonstrated to affect the probability of nest discovery by one such parasite, *Metopia sauteri* (Endo 1980; see also Weislo et al. 1985). In these studies as well as the present one, parasites were inactive in the early morning and late afternoon, times of lower ambient temperature and solar radiation. During the nesting season at Sagehen Creek, soil surface temperatures, measured by placing an unshaded mercury thermometer on the soil in direct sunlight, cycle dramatically from approximately 30.8°C up to 56.8°C and down to 36.3°C at 0900, 1400, and 1800 h, respectively (Rosenheim 1989). Both *Argochrysis armilla* and the parasitic flies studied by Evans et al. (1980) and Endo (1980) may develop gregariously, with many parasites possible in a single host cell; the parasites are much smaller than their hosts. A simple, but untested, hypothesis for asynchrony invokes different thermal constraints on activity due to pronounced size differences between host and parasite.

Regardless of the specific mechanism generating asynchrony of host and parasite, the existence of temporal refuges from parasites suggests a potentially important relationship between parental investment in nest provisions and vulnerability to parasites of the nests constructed by the resulting offspring. Parents determine, through the quantity of food provisioned, the size of the offspring produced (O'Neill 1985). In the only study of its kind to date, Willmer (1985b) demonstrated significant variation in the daily activity periods of *Cer-*

*ceris arenaria* females related to variation in female size: larger females foraged significantly earlier in the day while smaller females were able to continue foraging during the highest ambient temperatures when the physiological tolerances of the larger wasps were sometimes exceeded. If size-dependent variation in foraging activity is common, vulnerability to parasites may be usefully considered along with foraging and competitive abilities when analyzing costs and benefits of variable patterns of parental investment.

#### *Spatial density-dependence*

The increased probability of nest parasitism by *Argochrysis armilla* in areas of high host nesting activity operates against the formation of nesting aggregations. To what extent can this result be generalized within the solitary nest-building Hymenoptera? A review of field studies of spatially density-dependent parasitism (Rosenheim 1990) revealed examples of each of the three possible outcomes: direct density dependence ( $n=8$ ), density independence ( $n=4$ ), and inverse density dependence ( $n=2$ ). These diverse results were observed despite the fact that parasites foraged either independently of host density ( $n=2$ ) or concentrated in areas of high host density ( $n=4$ ). Variation in patterns of density dependence appeared to be generated by the interplay of different parasite foraging strategies and different host defensive strategies. Parasites may therefore favor either aggregated or dispersed nesting.

#### *Delayed nest provisioning*

The gradually declining time course of nest monitoring exhibited by *Argochrysis armilla* (Fig. 5) created a partial temporal refuge from parasitism and thus represents a new factor favoring the evolution of delayed nest provisioning and subsociality.

The first evolutionary step towards the temporal segregation of nest excavation and nest provisioning is a shift from a prey-nest behavioral sequence, in which the nest is excavated only after the prey has been captured, to a nest-prey sequence (Rosenheim 1987a). The second step is an increasingly delayed nest provisioning. Although the distributions of *Ammophila dysmica* hunting times were significantly skewed towards larger values compared to exponentially decaying distributions, the deviations were very slight (Fig. 6). Furthermore, the differences between the observed and expected distributions were non-significant for

hunting times  $\geq 1100$  min, when the refuge from parasites became significant in decreasing nest parasitism (Fig. 5). Thus, although the identity of the factor(s) causing the small deviations in hunting times from the expected distributions is unknown, the observed deviations appeared unlikely to have a significant effect on nest parasitism. Long hunting times are probably the result of the stochastic process of hunting and prey encounter and do not appear likely to be part of an evolved strategy of parasite avoidance by *Ammophila dysmica*.

An obligatory strategy of delayed nest provisioning appears inefficient unless work on additional cells or nests can be interposed between the excavation and provisioning of a given nest. Such a strategy of simultaneous activity at multiple nest sites is exhibited by several *Ammophila* spp. (reviewed by Hager and Kurczewski 1986), including *Ammophila azteca*, a host of *Argochrysis armilla*. For these *Ammophila* spp. the characteristic delays in nest provisioning may represent adaptations to reduce nest parasitism by *Argochrysis armilla* or other parasites that learn nest location. Why *Ammophila dysmica* continues to tend only a single nest at a time is unclear. This apparently ancestral trait may be favored by other selective forces, or the species' evolution may be genetically constrained.

Delayed provisioning may be a widely available defensive strategy for Hymenoptera attacked by parasites that learn nest location. Although the prevalence of locality learning is presently unknown, learning appears to be a component of the foraging strategies of a number of parasitic bees (Rosenheim 1987b; Wcislo 1987). However, temporal barriers may only be effective defenses for hosts that build unicellular or oligocellular nests. Specialized parasites of hosts building multicellular nests may not show decreasing nest monitoring over time. The pattern of decreasing nest attendance observed for *Argochrysis armilla* (Fig. 5a) may represent either (1) a limited memory or (2) a decision to terminate foraging at sites of low profitability. Selection against an indefinitely-long monitoring of a given nest by *Argochrysis armilla* may be strong for two reasons. First, nests may be completed without the parasite's detection, due to asynchrony of host and parasite (Fig. 1) and possible limitations of a parasite's ability to monitor several nests simultaneously (Rosenheim 1987b). Second, some nests abandoned by *Ammophila dysmica* during excavation continue to be monitored by *Argochrysis armilla* (Rosenheim 1988, unpublished data), and approximately 12% of all fully-excavated nests are never provisioned

(Rosenheim 1987a). Selection may favor longer-term monitoring behavior for parasites of multicellular nests. Multicellular nests may therefore accrue a progressively increasing number of nest-monitoring parasites over the nesting season (Eickwort et al. 1977).

The construction of unicellular or oligocellular nests is widespread in the Hymenoptera (Evans 1957, 1966; Iwata 1976; Michener 1974; Evans and O'Neill 1988). Previous observations of bees and wasps that distribute their offspring in several distinct nests have led several authors to suggest strategies of "risk spreading" (Alcock 1982; Elliott et al. 1986; Frohlich and Tepedino 1986; Evans and O'Neill 1988); the currently proposed hypothesis of escape from learning parasites is complementary to this risk spreading hypothesis. The suggestion that learning parasites select against the construction of multicellular nests should be testable by determining if the relative risk of parasitism increases in sequentially constructed cells of a single nest.

I have attempted to show in this study how the behavior of *Ammophila dysmica* modulates the impact of the nest parasite *Argochrysis armilla*. In the absence of balancing pressures, natural selection will tend to reinforce those aspects of host behavior that reduce the probability of nest parasitism, namely the excavation of nests in the early morning or late afternoon, the selection of nest sites in areas of low conspecific nest density, and the provisioning of nests long after nest excavation. Parasites using foraging strategies different from that of *Argochrysis armilla* appear likely to produce a different set of selection pressures. Part of the diversity of evolutionary trends within the Hymenoptera may reflect the multiplicity of selective forces in operation (Evans and O'Neill 1988), including the many forms of parasite pressure.

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