

## INTRASPECIFIC PARASITISM AND NESTING SUCCESS IN THE SOLITARY WASP *AMMOPHILA SABULOSA*

by

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(With 4 Figures)

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### Introduction

Intraspecific parasitism is widespread in solitary aculeate wasps and bees, ranging from the probably opportunistic theft of prey from prey-laden females outside the nest (*e.g.* EVANS, 1957; KURCZEWSKI & KURCZEWSKI, 1984) to usurpation of the nest structure (*e.g.* COVILLE & COVILLE, 1980; COWAN, 1981), theft of prey from inside the nest (*e.g.* EBERHARD, 1972; ALEXANDER, 1986) or brood parasitism, in which the parasite opens a completed cell and replaces the host egg with an egg of her own (*e.g.* NEWCOMER, 1930; MATTHEWS, 1965; EICKWORT, 1975). Intraspecific parasitism has rarely been systematically documented (exceptions are EBERHARD, 1972, 1974; BROCKMANN & DAWKINS, 1979; BROCKMANN, 1980, 1985; see also EICKWORT, 1975; MYERS & LOVELESS, 1976). It is hard to detect unless females are individually marked, and brood-parasitized nests may be indistinguishable from unparasitized ones after parasitism has occurred. Nevertheless, intraspecific parasitism is probably a significant cost of coloniality in some solitary bees (EICKWORT, 1975; MYERS & LOVELESS, 1976).

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The range of nesting behaviour found within the tribe Ammophilini (Sphecidae, Sphecinae) represents in a sense a microcosm of early behavioural evolution within the Sphecidae (EVANS, 1959). Most of the 187 described *Ammophila* species (BOHART & MENKE, 1976) excavate their unicellular nests before prey capture, but in several species (ROTH, 1928; HICKS, 1934; WEAVING, 1984; ROSENHEIM, 1987a) and in most species of the closely related genus *Podalonia*, this sequence is reversed, as in the pompilids and unlike almost all other sphecoids. Most *Ammophila* species are mass provisioners, some placing only one large prey item in each cell. The cell is completely provisioned and permanently closed before the wasp egg hatches. Females of other species, however, provision progressively, permanently closing each cell only when the wasp larva is quite large and maintaining more than one nest simultaneously (BAERENDS, 1941; EVANS, 1965; HAGER & KURCZEWSKI, 1986). In this paper the nesting behaviour and bionomics of *Ammophila sabulosa* (L.) are described with particular emphasis on intraspecific parasitism and its importance relative to other mortality factors. Provisioning strategies and alternative nesting strategies in *A. sabulosa* will be discussed elsewhere (FIELD, in press).

## Methods

### *Study site.*

The study site was a sandy heathland ride, approximately 40 m wide, running between a huge Scots pine/Corsican pine plantation (Forestry Commission) and a railway embankment at Santon Downham, Norfolk, U.K. (map reference TL 818883). I have recorded nearly 200 solitary wasp and bee species at the site. *A. sabulosa* nests were restricted to a bare or sparsely vegetated sandy path (mean width of nesting area = 5.25 m) running parallel to the railway and separated from it by an approximately 5 m-wide grass verge. Between the path and the forest edge was an approximately 22 m-wide belt of scrub, then a hard sand track and another grass verge. The scrub was dominated by birch saplings, patches of *Calluna* and *Erica*, clumps of tall grasses and small pine stumps.

Preliminary observations were made in 1984 but the main research periods were the summers of 1985 and 1986. The major observation area in 1985 was Site A, a 70 m length of sandy path within which there were three sections totalling 40 m bare enough for nesting. Site A was separated from the next nesting area along the path, Site F, by 80 m of short, dense vegetation in which very few females nested. Between 23 June and 11 July wasps were observed at Site A, Site F and Site NP, a 16 × 57 m nesting area a further 420 m along the path from Site F. From 13 July until the end of the nesting season (30 August) observations were restricted to Site A.

In 1986 the study site was a 36 m-length of sandy path within Site F. This was barer and more homogeneous than Site A, containing no areas unsuitable for nesting. Most of the half nearest the scrub was covered by the moss *Polytrichum juniperinum* (34% of total nesting area) on which females nested with no apparent difficulty. At both ends of Site F the sand became loose and was little used for nesting, but Site F was more arbitrarily defined than Site A. At least one female nested both inside and outside it in 1986. Wasps were observed from 21 June to 6 August but there was very little female activity after 17 July because of unfavourable weather and a low initial density.

### *Marking.*

In both years all *A. sabulosa* females which could be found during the first few days of favourable weather after emergence were individually marked on site: 40 females at Site A in 1985, 38 at Site F in 1986. Each wasp was lightly anaesthetized using carbon dioxide, weighed to the nearest 1 mg on an electric microbalance (UNWIN, 1980) and marked with a unique colour-combination of three enamel paint dots applied to the dorsal surface of the thorax. Wasps were held in shade until completely recovered and released approximately 30 minutes after capture. Approximately half of all marked females were seen again on subsequent days and there were no noticeable effects of marking. Marks generally persisted through the season. Five females lost one or two spots each but could be identified from their nest associations. After the initial marking periods additional females, including those of the second generation, were marked when they were first seen: an additional 43 females by 29 August 1985 and 17 females by 17 July 1986. Marking was highly successful: 81/92 nests provisioned at Site A in 1985 (after 12 July) and 95/102 at Site F in 1986 belonged to marked females. Each female dug all of her burrows within a fairly short length of path (maximum = 21 m), allowing individuals to be followed throughout the season.

### *Data collection.*

Wasps were observed on almost every warm, sunny day during the study periods, as well as on many less favourable days, and observations covered approximately two-thirds of the total time during which there was any female activity. The positions of nests were permanently marked and in 1986 all nests were mapped. Females were observed by using 7 × 22 binoculars with which their marks could be distinguished without recapture. I attempted to observe all activities at marked nests by continuously walking around the edge of the observation area, but the lengths of path involved, necessitated by relatively low nest densities, meant that all nests could not be watched simultaneously. Nesting activities, particularly provisioning and prey theft, occur rapidly and some events were inevitably missed.

Six days after digging or three days after provisioning each nest was excavated and its contents recorded. Prey items were weighed to the nearest 1 mg. In 1984 no nest was active for more than six days except during unfavourable weather. When such weather occurred during 1985-6 nests were excavated correspondingly later.

Statistical tests are two-tailed with the significance level set at  $P = .05$ . Standard deviations (s) and sample sizes (n) are given.

## Results

### General nesting biology.

The non-parasitic *A. sabulosa* nesting cycle is shown in Fig. 1. A female digs an oblique burrow in the sand, 2.5-4.5 cm long, ending in a roughly oval horizontal cell 1-4 cm below ground (Fig. 2). Approximately half (47%) of all cells ( $n = 212$ ) are provisioned with one large paralysed caterpillar (single provisioning) and half with 2-5 smaller ones (multiple provisioning). Large prey are carried to the nest on foot, small prey often in short, low flights. After digging or provisioning, the female invariably closes the nest using tiny pebbles and sand. The entrance is filled level with the surface and the outside of the closure smoothed until it is invis-

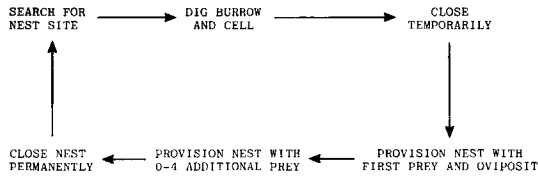


Fig. 1. Nesting cycle in *A. sabulosa* (simplified).

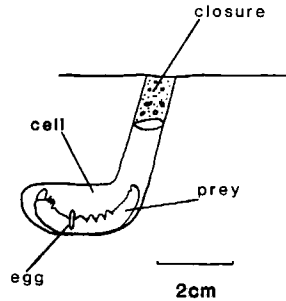


Fig. 2. Diagram of an *A. sabulosa* nest.

ble to the human eye. Then, if provisioning is complete, the female places camouflaging debris (pine needles, pebbles etc.) over the entrance, unless it is in completely bare sand. Thus, the nest is always closed in her absence, and must be re-opened each time she arrives with prey. Many burrows are abandoned (never provisioned). Females never maintain more than one nest simultaneously. A long-lived female may provision many nests during the summer, depending on the weather (maximum number observed = 10). Usually, females are active only in direct sunlight.

The egg is invariably attached to the first caterpillar placed in the cell, and cells are almost always mass provisioned. The egg hatches 2-7 days after oviposition, depending on temperature, and development from oviposition to the end of cocoon spinning can occur within eight days in hot weather.

Nest density was low. Integrating over time, a minimum estimate of average nest density at Site F (190 m<sup>2</sup>) in 1986 was 0.55 provisioned nests per m<sup>2</sup> (up to 17 July). However, each nest is active for only 1-7 days and even during ideal weather (6-11 hours activity per day) average

active nest density was only 0.07 per m<sup>2</sup> (n = 12 days, range 0.026-0.092).

### Nesting success.

Table 1 summarizes data obtained from nest excavations and direct observation. Intraspecific parasitism was the major mortality factor affecting eggs in *A. sabulosa* nests. Of 191 nests seen provisioned, at least 54 (28.3%) were parasitized by conspecifics while only nine (5%) were parasitized by dipterans. Approximately 67% of eggs laid by females in their own nests survived.

#### 1. *Intraspecific parasitism.*

*A. sabulosa* females often searched in the nesting area. Searching females walked, often with short, low flights at intervals, continuously examining the substrate. They sometimes stopped to examine particular spots more closely with their antennae and mandibles. Searching often ended when a female began to dig a new nest. Alternatively, she might find another female's nest. When within 3-5 cm of a closed nest she would suddenly stop, her vibrating antennae touching the substrate, then frantically dig at the adjacent sand. She usually found the nest entrance within seconds and immediately began digging through the closure. On 83 occasions during 1985-86 I saw females (parasites) open nests belonging to other females (hosts). Such nests were either empty (31/83) or contained one or more prey plus an egg laid by the nest owner (52/83). There were four main outcomes of opening a nest.

##### a. Brood parasitism.

Brood parasitism (Fig. 3) occurred when the parasite removed the host female's egg, replaced it with her own and re-closed the nest. The following detailed description is based on 26 observations.

Once through the closure, the female quickly pulled the prey out one at a time. She held the last one half out of the burrow while she bit at successive points along its body (Fig. 3c). When she reached the egg she usually ate it, but sometimes briefly held it in her mandibles then wiped it off with her front legs or carried it into mid-air and dropped it. Some eggs were apparently removed while the prey were still in the cell, though the prey were always subsequently pulled out. A minority (6/23) of eggs was removed only once the prey were completely outside the burrow. After egg removal the female often sat holding prey outside the nest

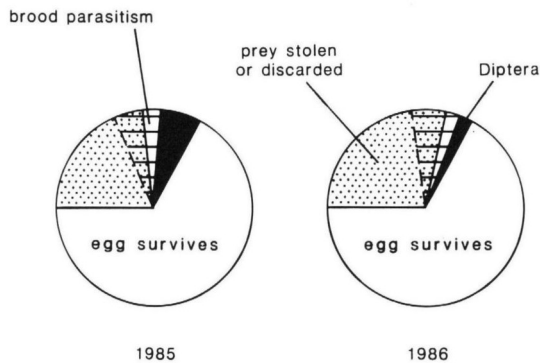
TABLE 1. Mortality factors affecting eggs in *A. sabulosa* nests

	Frequency		Percentage	
	1985	1986	1985	1986
Nests provisioned	103	88	100	100
Nests from which prey stolen or discarded <sup>1)</sup>	24(5)	25(4)	23(5)	28(5)
Nests brood parasitized but no prey stolen <sup>2)</sup>	3-9	2-9	3-8	2-9
Nest parasitized by dipterans	7	2	7	2
Eggs surviving	63-69	52-59	62-67	60-67

<sup>1)</sup> Bracketed figures are nests known to have been brood-parasitized before prey disappeared.

<sup>2)</sup> Lower estimate represents nests known to have been brood-parasitized without subsequent prey disappearance. See text for upper estimate.

Pie charts present the data in Table 1 diagrammatically, using the lower estimates for brood parasitism. Dashed lines indicate that some nests from which prey disappeared had previously been brood-parasitized. See text for details.



and/or carried prey about and/or repeated the biting behaviour and/or removed soil from the burrow (Fig. 3d). She also cleaned her mouthparts by biting the ground or vegetation and usually stung the prey at least once. Eventually, sometimes immediately after egg removal, she replaced the prey (Fig. 3e-f) and re-closed and camouflaged the nest (Fig. 3g). She oviposited on the first item replaced and usually took out soil before and after each replacement. Brood parasitism lasted an average of 32.3 minutes ( $n = 13$ ,  $s = 8.9$ , range 17-50). This comprised about 8 minutes before prey removal, 7 minutes during which prey were outside

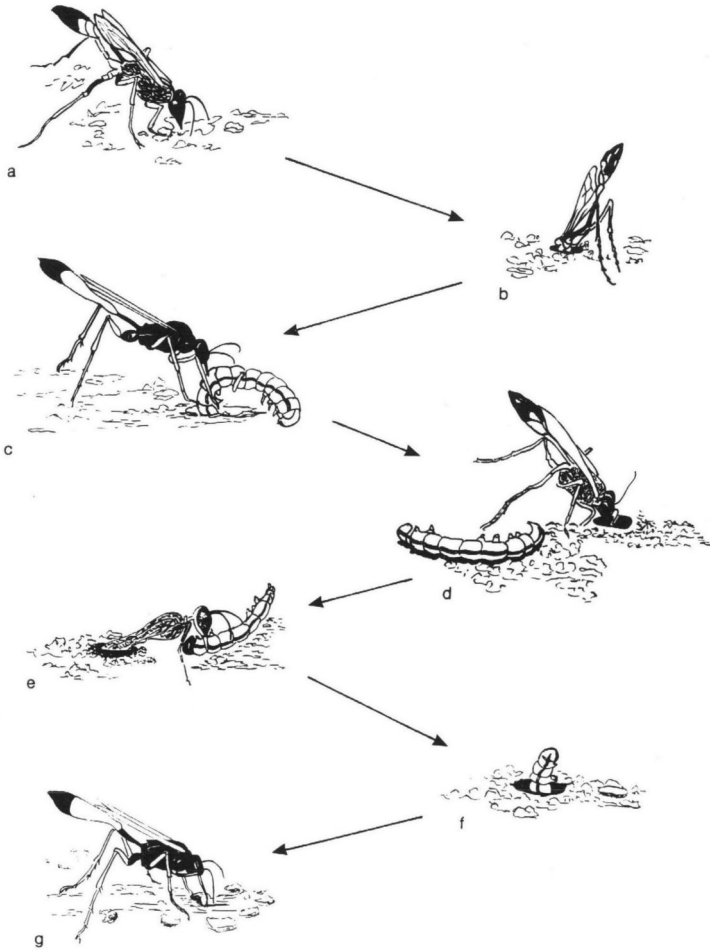


Fig. 3. Brood parasitism in *A. sabulosa*. a, parasite detects closed nest entrance; b, digs through closure; c, about to remove egg; d, removes soil from burrow; e-f, replaces prey; g, re-closes nest.

and an average of 15.4 minutes for re-closure, which did not differ in duration from permanent closure after provisioning (U-test, NS).

In 3/13 cases in which the host nest was multiply provisioned, one of the prey was not replaced. It was left on the sand near the re-closed nest containing the others. One nest contained a wasp larva when it was brood-parasitized. Most nests are probably no longer detectable when the larva emerges (see below), but the nest concerned was unusual in that

it was provisioned with the fourth prey item three days after the first, by which time the larva was feeding. Soon afterwards another female opened the nest. She placed the first three prey adjacent to the burrow entrance but left the fourth 10 cm away bearing a small wasp larva. After replacing the first three items she began searching for a pebble with which to begin closing. She came across the fourth caterpillar and, extraordinarily, carried it back to the entrance and replaced it without disturbing the wasp larva. The three intact prey were subsequently stolen by other females (see below), but four other nests excavated each contained two eggs or larvae on separate prey items. Two were reared, and in both cases the larger larva finished its prey item first then ate the smaller larva. Similar results were obtained experimentally by EBERHARD (1974) in *Trigonopsis*.

b. Discarding.

Discarding (10 observations) occurred when the parasite pulled out the prey, destroyed the host egg, but then departed without ovipositing, after up to 45 minutes at the nest. The prey were left on the sand and the nest re-closed very quickly and loosely or ( $n = 2$ ) left open. A caterpillar still bearing an egg was sometimes taken in and out of the nest three times before egg removal and departure. In two instances one caterpillar was discarded from the nest but the other(s) left inside, probably still bearing the host egg. Two females discarded after single parasitic flies had sat a few centimetres from the nest entrance, but another female completed brood parasitism after a fly entered the nest twice and probably larviposited. There were no obvious reasons for the other eight discardings.

c. Theft.

Theft ( $n = 15$  observations) occurred when the parasite pulled out one of the prey, removed the host egg if one was present, then immediately carried the prey to her own nest, an average of 6.1 m away ( $n = 15$ ,  $s = 3.63$ , range 0.8-13.9).

A stolen caterpillar was usually carried from the host nest rather rapidly. The thief would stop a short distance away, often in vegetation, and bite and often sting the prey, sit nearby it, and clean her mouthparts on the ground or vegetation, similar to the behaviour of females with prey outside a nest during brood parasitism. She would carry it on to her own nest only after several (maximum = 13) minutes.



Four females seen stealing from multiply provisioned nests each took the first prey item pulled out, leaving the other(s), probably bearing an intact egg, in the open burrow. A fifth female, however, took out two prey, removed the egg from one and stole it, leaving the other on the sand. None of these females returned to steal the remaining prey, and no female was ever seen stealing more than one caterpillar from the same nest, though multiply provisioned nests from which prey were stolen almost always (24/27) lost all of their prey eventually, at least sometimes to more than one female. The host egg was always removed when singly provisioned prey were stolen.

Theft occurs so quickly that it is easily missed. The mean time between starting to open the host nest and departing with stolen prey was 7.4 minutes ( $n = 7$ ,  $s = 3.7$ ). There is no way of knowing whether a female arriving at her nest with prey has stolen it or caught it herself unless she is observed taking it from another nest. The host burrow, however, is invariably left open by the thief, though the host eventually re-closes it, and no other agency ever led to the complete disappearance of previously provisioned prey. Discarded prey were visible on the sand adjacent to the nest entrance.

Females sometimes took discarded prey which they came across in the nesting area (4 observations). This occurred extremely rapidly as it did not involve egg removal or opening another female's nest. Freshly discarded prey were sometimes rejected (4 observations), even by females with nests, and partially desiccated prey which had been left outside overnight were never taken.

#### d. Empty nests.

If the host nest was empty (31 observations), either not yet provisioned ( $n = 9$ ), already stolen from ( $n = 11$ ), or abandoned, the parasite entered briefly then invariably loosely re-closed and departed. The whole operation lasted 1-5 (mean = 2.2) minutes. Four females returned and re-opened nests that they had previously found empty. Two found that the nest had since been provisioned by the host, and stole prey. Five females which opened empty nests had previously stolen from them. A nest could be 'checked' by several different females, or by the same female more than once, on one day. One nest, stolen from on 25 July 1985, was re-opened by three different females on 1 August, at 13.35, 13.55 and 14.30 (the same female), and 14.50. Empty nests were re-closed so quickly that the frequency with which they were opened will have been underestimated.

One other rare outcome of opening an empty nest was nest renovation. Between four and seven of the empty nests opened by parasites without nests of their own had been abandoned by their owners up to six days earlier. Three parasites, instead of re-closing the nest, removed some soil and subsequently provisioned it. In each case the original owner had by then started a new nest.

## 2. *Characteristics of intraspecific parasitism.*

### a. Strategies of individual females.

Individual females both provisioned their own nests and parasitized those of other females. Of 32 marked females active for at least 40 hours of observation, 24 opened at least one other female's nest. Thirty-one dug one or more nests of their own and provisioned them with prey which were not known to have been stolen. One female dug no nests and opened no nests.

### b. Clumping of parasitism events at certain nests.

Once a nest had been brood-parasitized, the prey were significantly more likely to be stolen or discarded (by a different female) than were prey in unparasitized nests (Table 2). Prey were eventually stolen or discarded from 14/19 (74%) nests at which I observed brood parasitism but from only 39/177 (22%) nests at which brood parasitism was not observed. Some nests were brood-parasitized more than once, each time by a different female (Table 3). Two nests were brood parasitized four times (four different females) before the prey were eventually stolen by a fifth female. Combining data from both years, the distribution of observed brood parasitisms among nests (Table 3) was significantly different from a Poisson distribution ( $\chi^2 = 10.03$ , d.f. = 1,  $P < .01$ ). The number of nests brood-parasitized more than once was greater than expected, despite the fact that no further brood parasitisms could occur after prey theft. In total, only 5/29 (17.2%) eggs laid by brood parasites survived (Table 3).

### c. Timing of parasitism.

Brood parasitism, theft and discarding almost always (39/41) occurred on the same day as the previous activity at the host nest (provisioning by the host or a previous parasitism), and a median of only 64.5 minutes later (Fig. 4,  $n = 40$ , range 7-1321). There was no significant difference between times for first ( $n = 24$ ) and second or subsequent ( $n = 16$ ) parasitisms (U-test, NS).

TABLE 2. The effect of brood parasitism on the probability of prey theft or discarding

a. 1985

Nests	Prey eventually stolen/discarded	Prey not stolen	Total
Brood parasitism observed	8	3	11
Brood parasitism not observed	19	76	95
Total	27	79	106

b. 1986

Nests	Prey eventually stolen/discarded	Prey not stolen	Total
Brood parasitism observed	6	2	8
Brood parasitism not observed	20	62	82
Total	26	64	90

1985:  $\chi^2$  (with Yates' correction) = 11.8,  $P < .001$ . 1986:  $\chi^2 = 6.8$ ,  $P < .01$ . Combined data:  $\chi^2 = 23.2$ ,  $P < .001$ .

TABLE 3. Frequency of intraspecific parasitism at individual nests

No. times nest brood parasitized	Frequency		No. from which prey eventually disappeared	
	1985	1986	1985	1986
0	95	82	19	20
1	9	5	6	4
2	1	1	1	1
3	0	1	0	0
4	1	1	1	1
Total eggs laid by brood parasites	15	14		
Surviving eggs	3	2		

## d. Estimating mortality due to intraspecific parasitism.

The frequency of prey disappearance is easily obtained by excavating nests. If a nest which I saw being provisioned contained an empty cell when excavated I assumed that the prey had been stolen or discarded, even if parasitism was not actually observed. Usually, I at least arrived in time to see the characteristic large hole left by the thief. Prey disappeared from 49/191 (25.7%) nests (Table 1). Nests at which I observed digging but not provisioning are excluded from Table 1, whether or not

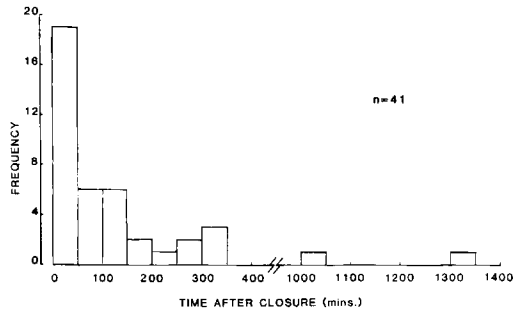


Fig. 4. Frequency distribution of time intervals between the start of intraspecific parasitism and the end of the previous activity at the host nest.

they contained prey when excavated. Empty cells excavated from such nests could indicate either burrow abandonment or unobserved theft.

It is harder to allow for unobserved brood parasitism since this does not alter a nest's contents or appearance. Fourteen out of 191 (7%) nests were known to have been brood parasitized at least once (Table 1), of which five were not subsequently stolen or discarded from. The lower estimate of the number of nests brood-parasitized but not stolen from in Table 1 represents these five nests. A few brood parasitisms must have gone unnoticed. If one assumes that all nests from which prey are stolen have previously been brood-parasitized, an estimate of the number of successfully brood-parasitized nests is:

$$[D.(1/P)] - D = [24.(1/0.75)] - 24 \text{ in 1985}$$

where D = number of nests from which prey were stolen or discarded, P = estimated probability of theft from a brood-parasitized nest (15/20 = 0.75, as above). This is the higher estimate in Table 1. The true figure certainly lies nearer the lower estimate, which is the one used in the pie charts. Prey were stolen from some nests which had undoubtedly not been brood parasitized, and brood parasitism was unlikely to go unnoticed because of its long duration, except when I was absent from the site.

### 3. *Interspecific parasitism.*

*Podalonia affinis* (K.) (Ammophilini) also provisioned unicellular nests with caterpillars at Santon Downham. It is a larger species which was much scarcer than *A. sabulosa*. It provisions nests singly, usually with

large 'cutworm' noctuid larvae (personal observations; PALMER & STELFOX, 1931), but 2/13 prey which I excavated from nests were *Eremobia ochroleuca*, a smaller species commonly utilized by *A. sabulosa*. I saw one of the *Eremobia* being stolen from an *A. sabulosa* nest, and another *P. affinis* female opened and re-closed an empty *A. sabulosa* nest.

I also once observed an *A. sabulosa* female brood parasitize a *P. affinis* nest, though she had great difficulty pulling the large noctuid to the surface. *A. sabulosa* females can hardly carry prey of the size used by *P. affinis* (personal observations), but one *A. sabulosa* nest was provisioned with a 623 mg noctuid which might have been stolen from a *P. affinis* nest.

#### 4. *Other interactions between females and prey theft outside the nest.*

Females lead extremely solitary lives. They sometimes met while walking in the nesting area, but noticeable interactions occurred only when one of them was at a nest or was carrying prey. Theft of prey during provisioning or transport to the nest (excluded from Table 1) was rare, occurring during only two out of nearly 200 cases where transport from the edge of the nesting area was observed. Ferocious fights lasting 5-15 seconds occurred when females came across prey-laden conspecifics ( $n = 2$ ) or prey which was about to be provisioned ( $n = 2$ ). The pair rolled in a ball, biting and kicking, until one of them departed leaving the other with the prey. When the original owner lost the fight ( $n = 2$ ) she subsequently approached the thief 2-5 times, but always flew away when chased, eventually not returning.

Females were also approached while they were closing nests after provisioning ( $n = 4$ ) or brood parasitism ( $n = 1$ ), or were in mid-parasitism ( $n = 5$ ). Usually the 'intruder' left when chased once or twice, but sometimes continued to make approaches for up to 50 minutes. After she departed the owner sometimes remained at the nest, apparently guarding it, for an unusually long time and once for over an hour. In two instances a closing female was eventually driven off after a short fight, and the intruder then re-opened the nest and brood-parasitized it or stole prey.

#### 5. *Miltogrammine parasitism.*

Miltogrammine flies (Diptera, Sarcophagidae) are major natural enemies of ground-nesting solitary wasps (EVANS, 1962, 1966, 1970; EVANS & WEST-EBERHARD, 1970) and usually larviposit onto prey or into burrows, particularly during provisioning (*e.g.* WCISLO, 1984; SPOFFORD *et al.*, 1986). In both years miltogrammine parasitism was of minor importance compared with mortality due to intraspecific parasitism (Table 1).

a. Miltogrammine behaviour at Santon Downham.

In 1985 miltogrammines (*Metopia* species) were common in hot weather at Site A, but were less common in 1986. They often watched digging females from nearby perches and at some point usually entered the burrow or sat just inside the entrance while the female was below ground. Some digging or closing females chased them away or abandoned digging, but on other occasions flies were ignored even when they moved directly under the female's body into the burrow. Entries by flies during digging never resulted in successful parasitism.

Two successful larvipositions were witnessed. In each case a fly sat on a nearby stone while a female re-opened her nest and pulled in prey. After she had been inside for a few seconds the fly flew into the entrance and sat just below the surface for five seconds, then flew away. *Metopia argyrocephala* (Meigen) was reared from one of these nests. A third case involved a provisioning *P. affinis* female which had begun to re-open when a second female noticed her. During the ensuing fight a fly hovered briefly over the prey lying on the sand. After the fight the original owner provisioned her nest with the prey.

When excavated, parasitized cells contained 1-3 fly maggots. Tiny maggots were usually on the wasp egg, which they probably ate, but larger maggots fed underneath the prey, especially in the folds of cuticle at the abdominal leg bases. The wasp larva never developed. The prey became blackened and smelly and the maggots burrowed into the soil to pupate. One second generation *M. argyrocephala* emerged on 13 August, 1985, and three others plus one *M. campestris* (Fallén) emerged after overwintering. One *M. campestris* was reared from a *P. affinis* nest. Though common at the site, *Senotainia conica* (Fallén) was never observed at *A. sabulosa* nests.

b. Cell cleaning.

After digging through the temporary closure, some provisioning females removed soil from inside the nest before pulling in prey. Similarly, females took 0-20 soil loads out before beginning to re-close. Similar behaviour in other species, termed cell-cleaning, is associated with the presence of flies and can result in maggot removal (HAGER & KURCZEWSKI, 1986; ROSENHEIM, 1987a).

Observations from two nests suggest that females occasionally discard prey from their own nests, possibly associated with the presence of flies. In one case a miltogrammine watched a female re-close her nest after

provisioning it with the first prey item, and sat on the entrance after she had departed. When she arrived with the second caterpillar, instead of taking it in directly she pulled out the first item which bore a collapsed wasp egg. She carried it around for several minutes, when a miltogrammine briefly entered the nest. She eventually abandoned the second item and reclosed the nest containing the first. Another caterpillar bearing a collapsed egg was discarded from a second nest by its owner, but the whole event was not observed. A third nest, however, contained two maggots when excavated, on the husk of the first of three prey. They were too large to have been larviposited during the final provisioning event, yet the female had not removed them.

#### 6. *Other mortality factors.*

Mortality factors operating after eclosion are largely unknown. The egg was missing from 10/148 (7%) cells containing prey and no parasites when excavated, though one may have been parasitized by miltogrammines and three others may have had other prey stolen from them. In an additional 5/148 cells the egg had shrivelled up. One female lost her prey when she carried it over a large ant nest within Site A. Losses during prey carriage before reaching the nesting area are unknown.

Inspections and host responses to intraspecific parasitism. A female periodically inspects her own nests from outside. She lands on the nesting area and moves in short flights to the entrance, stops for 2-3 seconds, antennae vibrating and mouthparts touching the closure, then circles the nest and flies away. Females mainly inspect nests which they later provision, but also burrows which they have abandoned up to 13 days earlier, sometimes even when they have since completed other nests. They also inspect nests completed up to two days before and nests which they have previously parasitized or found to be empty. Sometimes the female smooths the closure a little or places an extra piece of camouflaging debris.

When an inspecting female discovers an open entrance from which her prey, or prey in a nest she has brood-parasitized, have been stolen, she enters briefly, sits nearby for 1-2 minutes then loosely fills the top of the hole with tiny pebbles. She never re-provisions the nest.

Casual observations suggested that intervals between inspections are usually at least 90 minutes and often over 150 minutes. It was therefore relatively unusual for inspecting females to interrupt intraspecific parasitism. Only 9/38 (24%) continuously observed parasitisms (12

thefts, 26 brood parasitisms and discards) were interrupted by hosts. Additionally, one female arrived just as another appeared to be about to open her nest, causing the potential parasite to depart. In 2/9 interruptions the parasite had only partly opened the nest, and was driven off by the host which then re-closed it. In the remaining seven cases the host was easily driven off by a parasite which had already removed prey from the nest, and parasitism continued to completion (two thefts, four brood parasitisms, one discard). One host subsequently returned and 'helped' a brood parasite re-close her nest. After the other three brood parasites had left, the hosts returned. One simply inspected the closure then flew off, though she did not continue to provision the nest. Another re-opened her nest, pulled out the prey, removed the parasite's egg and replaced it with another of her own, but did not replace a caterpillar discarded during parasitism. The third host dug through the closure but then backed out and re-filled. This was after the unique parasitism in which a host larva was replaced intact by the parasite (above).

Two females replaced prey which they found discarded outside their nests. One found both prey lying outside an open nest which she had previously closed permanently; the other found one of two prey items, the other having been stolen. Both inspected within 40 minutes of parasitism and carefully re-closed their nests after prey replacement and oviposition. In four other instances a female found her nest open with all but one of the prey still inside, including one bearing her egg. A single caterpillar had been stolen ( $n = 3$ ) or discarded ( $n = 1$ ) from each. All four females re-closed their nests, though the discarded prey was not replaced. A larva developed successfully in one of these nests from which no further thefts occurred. Of 18 caterpillars discarded during the two years, 11 were carried off by ants, four were stolen within ten minutes of being discarded (above) and three were replaced by hosts. Nest owners never added new prey to parasitized nests.

Hosts did not usually appear to respond when they inspected after the completion of brood parasitism. Similarly, a nest which was opened by another female before provisioning would still be provisioned by its owner. In one exceptional case the host returned five minutes after a brood parasite had left and 're-parasitized' her nest, though it is possible that she had returned during parasitism without being noticed.

## **Discussion**

Nesting success and intraspecific parasitism.

The most striking aspect of the data is the large proportion of nests parasitized by conspecifics. A brood parasite gains an entire provisioned



nest—food and shelter for her larva— which would have taken her an average of 8-10 hours of activity to complete herself. A thief gains a caterpillar which will partly or completely provision her nest. These are valuable resources, and there is little chance of successful defence or retaliation by the host, factors which in birds have been suggested to favour the evolution of kleptoparasitism (BROCKMANN & BARNARD, 1979). However, the density of freshly provisioned host nests is low, nests are difficult to detect and thieves cannot search selectively for nests containing large prey—empty nests are often opened.

Few systematic studies of sphecoids have reported significant levels of intraspecific brood parasitism or prey theft from nests. In *Trypoxylon politum* Say, 2% of nests are brood-parasitized and single prey items are discarded from 14% (BROCKMANN, 1980). EICKWORT (1975) found that 15.2% of cells in nest aggregations of the mason bee *Hoplitis anthocopoides* (Schenck) were brood-parasitized by conspecifics. There are relatively few previous reports of intraspecific parasitism in the well-studied genus *Ammophila*, probably partly because there have been few detailed studies of marked females. Brood parasitism has been observed twice in what may be a subspecies of *A. sabulosa* (TSUNEKI, 1968) and once each in *A. atripes* Smith, a *Podalonia* species and probably *A. aberti* Haldeman, in which host egg removal was not noticed (NEWCOMER, 1930; PARKER *et al.*, 1980; KROMBEIN, 1984). Only PARKER *et al.*'s observations involved marked wasps. Theft from one nest to another occurs in *Podalonia hirsuta* (Scop.) (STEINER, 1975), and another probable instance is recorded by TSUNEKI (1968). Theft from prey-laden females outside the nest has been observed in *A. aberti* and *A. harti* (Fernald) (PARKER *et al.*, 1980; HAGER & KURCZEWSKI, 1986).

The detailed studies of HAGER & KURCZEWSKI (1986) and ROSENHEIM (1987a) indicate that parasitic behaviour is rare and unspecialized in some *Ammophila* species (Table 4). *A. harti* (n = 4) and *A. dysmica* Menke

TABLE 4. Mortality factors affecting cells of three *Ammophila* species<sup>1)</sup>2)

Species	Intraspecific parasitism	Miltogrammine parasitism	Other natural enemies	Source
<i>A. harti</i> <sup>P</sup>	0.4-1.7 <sup>3)</sup>	4	1.5	HAGER & KURCZEWSKI, 1986
<i>A. dysmica</i> <sup>M</sup>	0.4-3.0 <sup>3)</sup>	5	31 <sup>4)</sup>	ROSENHEIM, 1987a
<i>A. sabulosa</i> <sup>M</sup>	28-34	5	0	This study

<sup>1)</sup> M = mass provisioner; P = progressive provisioner. <sup>2)</sup> Figures are percentages of cells known to have been provisioned. <sup>3)</sup> Discarding female could have been nest owner in all but one case. <sup>4)</sup> 29% due to *Argochrysis armilla*.

( $n = 3$ ) females occasionally discarded prey, usually bearing wasp eggs ( $n = 6$ ), but brood parasitism and prey theft from nests were never observed (HAGER & KURCZEWSKI, 1986; ROSENHEIM, 1987a). In *A. dysmica* a parasite (chrysidid) larva, miltogrammine puparia, and prey remains with larvae were also occasionally discarded ( $n = 4$  cells). Discarding females did not destroy wasp immatures, but some discardings may have involved nest owners themselves since females concerned were unmarked in all but two cases, both of which involved non-owners (HAGER & KURCZEWSKI, 1986; ROSENHEIM, 1987a). Some of the *A. dysmica* ( $n = 5$ ) and *A. harti* ( $n = 2$ ) nests were subsequently re-provisioned, by the discarding females themselves in *A. harti* (B. HAGER, pers. comm.). Re-provisioning by the host or parasite after discarding or theft was never observed in *A. sabulosa*, presumably reflecting the high risks involved in using a burrow which can be located by another female.

When *A. dysmica* females found other females' nests while searching for digging sites they occasionally partially removed then replaced closures, but usually simply dropped a few pebbles into the depressions over entrances (ROSENHEIM, in press). *A. sabulosa* females sometimes close *Cerceris arenaria* (L.) (Sphecidae) nest entrances with tiny pebbles. Parasite pressure and progressive provisioning are possible adaptive explanations for the absence of specialized parasitic behaviour. In *A. harti* the egg is laid on the first caterpillar, but other prey are added only after hatching and are rapidly eaten (HAGER & KURCZEWSKI, 1986). Thus, a parasite would often find no uneaten prey suitable for theft, and brood parasitism could occur only before the nest was provisioned with the second item. *A. dysmica* cells are mass provisioned, as in all of the ammophilines which exhibit specialized parasitic behaviour, but 29% of cells are parasitized by a chrysidid (ROSENHEIM, 1987a). Brood parasitism, particularly, would be likely to attract parasites because of its duration.

One anomaly in HAGER & KURCZEWSKI's (1986) data is that it can be calculated from their Table 3 that 21% of 239 provisioned nests were inexplicably empty when excavated within 2-3 weeks. Perhaps unobserved prey theft was sometimes responsible. The proportion of empty nests was highest when female density was highest.

#### Detection of host nests.

Closed *A. sabulosa* nests are invisible to the human eye and it seems likely that chemical stimuli are important in their detection by searching conspecifics, though experiments are clearly necessary to establish this.

Many searching hymenopterous parasitoids are 'arrested' by 'contact chemicals' deposited on the substrate by their hosts (VINSON, 1976; WAAGE, 1978). Occasionally, however, searching *A. sabulosa* females are visually attracted to females in the process of closing, or re-locate nests which they have previously opened before provisioning ( $n = 2$  observations) and perhaps monitored since. A female can certainly learn the locations of and regularly inspect 2-3 nests simultaneously. She never parasitizes her own nests except occasionally after brood parasitism by a conspecific.

The fact that parasitism almost always occurs soon after the previous activity at the host nest suggests that cues involved in nest detection derive from that activity and are short-lived. It is unlikely that nests become unsuitable for parasitism within a few hours of provisioning. The host egg often fails to hatch within 36 hours and even after hatching there are intact prey suitable for theft in multiply provisioned nests. The only nest parasitized after hatching was one at which provisioning was unusually delayed, and the three intact prey were all stolen. Searching females rarely ( $n = 3$ ) failed to open recently-closed nests which they detected. In *A. dysmica* discarding sometimes occurs 5-15 days after provisioning, but nests of this species are externally visible, and remain so after completion, except following heavy rain (ROSENHEIM, 1987a; pers. comm.).

The high frequency with which brood-parasitized nests were re-parasitized may reflect an accumulation of chemical stimuli during the 17-50 minutes spent at the nest by the parasite, or that certain nests are intrinsically easy to find, perhaps because of their locations. Brood parasites permanently closed and camouflaged host nests just as carefully as they did their own nests. If chemical accumulation is involved, one might also expect it to be detected by inspecting hosts.

#### Defence against parasitism.

The large proportion of *A. sabulosa* nests parasitized suggests that the evolution of effective anti-parasite behaviour would be strongly favoured, yet nest inspections were infrequent and females rarely succeeded in driving off parasites. One host 're-parasitized' her nest after interrupting brood parasitism, but hosts were apparently unable to detect that it had occurred after the event. They replaced discarded prey if they arrived before it was stolen, and re-closed nests containing undisturbed prey, though their larvae were then left with little food. Rarely, females

appeared to guard nests after permanent closure or after successfully repelling conspecifics.

In solitary wasps and bees with multicellular nests, completed cells are incidentally guarded while the female works on more recent ones, though she is still occasionally driven off by a parasite (*e.g.* MATTHEWS, 1965; EICKWORT, 1975; ALEXANDER, 1986). Males of some *Trypoxylon* species (Sphecidae) guard nests almost continuously in the absence of their mates (CROSS *et al.*, 1975; BROCKMANN, 1980; COVILLE & COVILLE, 1980), but male involvement in nesting is otherwise extremely rare in solitary aculeates. Preliminary observations of the pompilid wasp *Anoplius viaticus* (L.) suggest that unicellular nests can be successfully defended. Females provision successive unicellular nests within very small areas which they inspect every few minutes during hunting, repelling intruders which try to dig into completed nests. Similar territorial behaviour occurs in *Podalonia valida* (Cresson) (STEINER, 1975), females which attempt to re-open nests being consistently repelled by nest owners. In *A. sabulosa* an individual's successive nests are much further apart and harder to defend (1986: mean distance between successive nests dug by one female = 3.9 m, n = 52, range 0.01-18).

#### Miltogrammine parasitism.

The percentage of *Ammophila* cells parasitized by miltogrammines (Table 4) is low compared with other sphecids (*e.g.* PECKHAM, 1977; WCISLO *et al.*, 1985; SPOFFORD *et al.*, 1986). Larviposition can occur only during very short, infrequent periods when the nest is re-opened to provision, and maggots may be removed during cell-cleaning (HAGER & KURCZEWSKI, 1986; ROSENHEIM, 1987a). Some miltogrammines probably wait for prey-laden females at individual host nests or nest aggregations (SPOFFORD *et al.*, 1986; unpublished observations), but this strategy would be relatively unrewarding when attacking most mass provisioning *Ammophila* species. Most *A. sabulosa* and *A. dysmica* cells are provisioned with only one or two prey. Digging and provisioning, and successive provisioning events, are rarely separated by less than an hour and often occur on different days (FIELD, 1987; ROSENHEIM, 1987a), and nest densities are low. Some progressive provisioners use up to 12 prey per cell (HAGER & KURCZEWSKI, 1986), but maggots introduced after the wasp egg hatches are probably outcompeted or eaten by the wasp larva (HAGER & KURCZEWSKI, 1985). Other aspects of *Ammophila* nesting biology which may reduce cell parasitism are discussed by ROSENHEIM (1987a).

One specialized parasite that has overcome the difficulties of parasitizing *Ammophila* cells is *Argochrysis armilla* Bohart (Chrysididae) (Table 4). Female *Argochrysis* detect nests initially during the long, conspicuous digging phase, learn their locations and subsequently re-visit them at intervals, monitoring several nests simultaneously and ovipositing during host provisioning events (ROSENHEIM, 1987a, 1987b). *Argochrysis* eggs are not removed by cell-cleaning (ROSENHEIM, 1987a).

### Summary

The nesting behaviour of marked female solitary wasps, *Ammophila sabulosa* (L.) (Sphecidae), was studied over two seasons at a Norfolk heathland site. Females mass provisioned unicellular nests with 1-5 paralysed caterpillars. Intraspecific parasitism was the major mortality factor before the egg hatched — approximately 28% of eggs were destroyed by parasites. Parasites stole caterpillars to provision their own nests, replaced host eggs with their own eggs (brood parasitism), or simply discarded prey from host nests. Hosts were ineffective at preventing parasitism. Individual females both provisioned their own nests and parasitized those of other females. Parasitism usually occurred soon after the previous activity at the host nest. Parasitism events were clumped at certain nests, which were parasitized up to five times each. Once a nest had been brood parasitized, the prey were significantly more likely to be stolen or discarded than were prey in unparasitized nests, and only 17% of eggs laid by brood parasites survived. Circumstantial evidence suggests that chemical stimuli are important in detection of host nests by parasites.

High levels of intraspecific parasitism have rarely been reported in solitary wasps and bees, and parasitic behaviour is rare and unspecialized in some other *Ammophila* species. Parasitism by miltogrammine flies was of relatively minor importance in *A. sabulosa* as in other *Ammophila* species, probably because provisioning events, during which flies larviposit, are few and well separated in time.

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## Résumé

Le comportement de nidification de femelles marquées de la guêpe solitaire *Ammophila sabulosa* (L.) (Sphecidae) a été étudié pendant deux saisons à un site sur les landes de Norfolk (Angleterre). Les femelles approvisionnent leurs nids à cellule unique de 1 à 5 chenilles paralysées. La cause majeure de mortalité avant l'éclosion des oeufs était le parasitisme intraspécifique: environ 28% des oeufs furent détruits par les parasites. Les parasites volaient des chenilles pour approvisionner leurs propres nids, remplaçaient les oeufs de leurs hôtes par leurs propres oeufs, ou enlevaient simplement les proies paralysées du nid de l'hôte. Les guêpes hôtes étaient incapables d'empêcher ce parasitisme. Chaque femelle peut approvisionner son propre nid et parasiter ceux d'autres femelles. Le parasitisme avait généralement lieu peu après un approvisionnement par l'hôte. Les cas de parasitisme étaient plus fréquents pour certains nids, ceux-ci étant parasités jusqu'à cinq fois successivement. Les proies sur lesquelles des oeufs de parasites étaient pondus étaient significativement plus susceptibles d'être volées ou jetées hors du nid que les proies de nids non-parasités; 17% seulement des oeufs pondus par les parasites dans les nids des hôtes ont survécu. Des preuves indirectes suggèrent un rôle important de stimuli chimiques dans la détection de nids d'hôtes par les parasites.