

Nesting Behavior and Nest Distributions of *Ammophila gracilis* Lepeletier (Hymenoptera: Sphecidae) in Brazil

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Abstract.—*Ammophila gracilis* is a mass provisioner, supplying an egg with 1–2 geometrid caterpillars over 1–2 days before final nest closure. Nesting of marked wasps was observed at two sites in Belo Horizonte, Minas Gerais, Brazil. Nests at the more homogeneous site ($n=54$), an open dirt road, had a clumped distribution, compared to those at the other site ($n=30$) which consisted of a series of small patchy clearings. Adult wasps lived up to 84 days. Development averaged 56 ± 10 days. Seven nests were destroyed by miltogrammine flies (*Metopia* n. sp. nr. *sinipalpis*). Ant predation was suspected as the major cause of mortality for 59 nests that did not yield adult wasps or parasites. A distinctive “crouching” behavior displayed by nesting females when miltogrammine flies were detected is described for the first time.

INTRODUCTION

Sphecids in the genus *Ammophila* Kirby are all ground-nesting wasps that capture prey, especially naked lepidopterous caterpillars and symphytan larvae, to provision each nest where a single larva develops (Evans 1959; Powell 1964; Bohart and Menke 1976). However, larval weevils have been recorded as prey for *A. azteca* Cameron (Evans 1965). The complexity of nesting behaviors is noteworthy in this genus (Evans and West-Eberhard 1970; Tinbergen 1974; Field 1989), and is among the most diverse in the Sphecidae. The importance of ethological studies to the systematics of the group was demonstrated by Baerends (1941) and Adriaanse (1947), who discussed the inter- and intra-specific nesting behavior, and Rosenheim (1987), who also discussed the importance of prey-nest sequences, though Weaving (1989) stressed that prey-nest sequences in *Ammophila* do not always reflect the systematic relationships supported by morphology.

Members of *Ammophila* display a wide range of nesting tactics (discussed by Evans 1959; Powell 1964; Bohart and Menke 1976; Parker *et al.* 1981), including mass provisioning, in which one to a few caterpillars are put into a single nest over a period of 1–2 days; delayed provisioning, in which the last prey item is provided after egg eclosion; and progressive provisioning, in which they continue to reopen nests to provide food through much of larval life. The progressive-provisioning members, such as *A. harti* (Fernald), may maintain several nests in different developmental stages at one time (Baerends 1941; Evans 1965; Tsuneki 1968; Hager and Kurczewski 1986). Also, as Weaving (1989) pointed out, many mass provisioning species can be facultatively delayed provisioners due to inclement weather. Krombein (1984) discussed the general provisioning tactics for several species, including *A. laevigata* Smith (a mass provisioner of several prey items per nest) and *A. atripes* Smith (a mass provisioner of one large prey item per nest). *Ammophila* are

also noted for tool use, especially for using a pebble in the mandibles to push down and pack soil into their completed nests (Peckham and Peckham 1898; Evans 1959; Powell 1964; Tsuneki 1968). A classic account of nest building and provisioning in *Ammophila* and other wasps, including numerous outstanding, informative photographs, is provided by Olberg (1959). Many of the behaviors discussed in the present work are also illustrated with photographs for other *Ammophila* species in Olberg (1959).

We observed the nesting behavior of female *A. gracilis* Lepeletier, gathering information about their general habits of searching and nest construction, provisioning and nest closure, interactions with other insects, and nest distributions at two sites on the Pampulla campus of the Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil.

MATERIALS AND METHODS

The first site, which we will call "Prefeitura," was a 150 m long and 6–10 m wide, homogeneous, compact sand and dirt road (Fig. 1A) within a 3 hectare plot of land containing vegetation in secondary succession. The second study area, which we will call "Estação Ecológica," was a long trail with a series of small, patchy clearings (Fig. 1B), all within a 156 hectare research facility of 2nd growth vegetation. Details of the vegetation of Estação Ecológica are discussed by Martins and Almeida (1994) and Martins and Antonini (1994). Both sites had dense, grassy and shrubby vegetation along the edges. *Ammophila gracilis* was commonly encountered at both of these sites, at which we logged over 100 hours of observations at each from April to December 1993.

We spent the first few weeks making preliminary observations and marking and measuring female *A. gracilis*. They were hand netted and worked into a matchbox such that only their head and

upper surface of the thorax were exposed (see Fig. 9 of Martins and Pimenta 1993). Head and thorax widths were measured, and each wasp was marked on the mesothorax with three dots of acrylic, fast-drying paint, in a unique color combination. It was carefully noted where each was originally captured, and any subsequent sightings were noted as to exact location and date. Fifty-four wasps were captured and marked.

We carefully recorded female activities, including searching and nest building, prey handling and nest provisioning, nest plugging and camouflaging, breaks for taking nectar from flowers, and any interactions with other insects. In addition, we marked 84 nests (54 at Prefeitura, and 30 at Estação Ecológica) to identify the individual wasp and the date of her nest completion.

Upon seeing a wasp with prey, we followed to her nest. After the nest was finally provisioned and plugged, we placed a glass chip over the entrance (after Weaving 1989). After the chip remained unmoved for over a week, indicating that she probably has not returned and reexcavated the nest, we secured a marked plastic cup over the nest to capture whatever emerged.

During ongoing studies of various ground-nesting wasps and bees at the two sites (e.g. Martins and Almeida 1994; Martins and Antonini 1994), *A. gracilis* has been active during the period of February through September. However, they have been noticeably absent during the rainy season of October through January, though the nature of this apparent dormancy remains a mystery.

All values presented are expressed as the mean \pm standard deviation. Voucher specimens of *A. gracilis* have been placed in the "Laboratório de Ecologia e Comportamento de Insetos" at UFMG, Belo Horizonte, Minas Gerais, Brazil, and in the Illinois Natural History Survey, Urbana, Illinois, USA. Voucher specimens of the

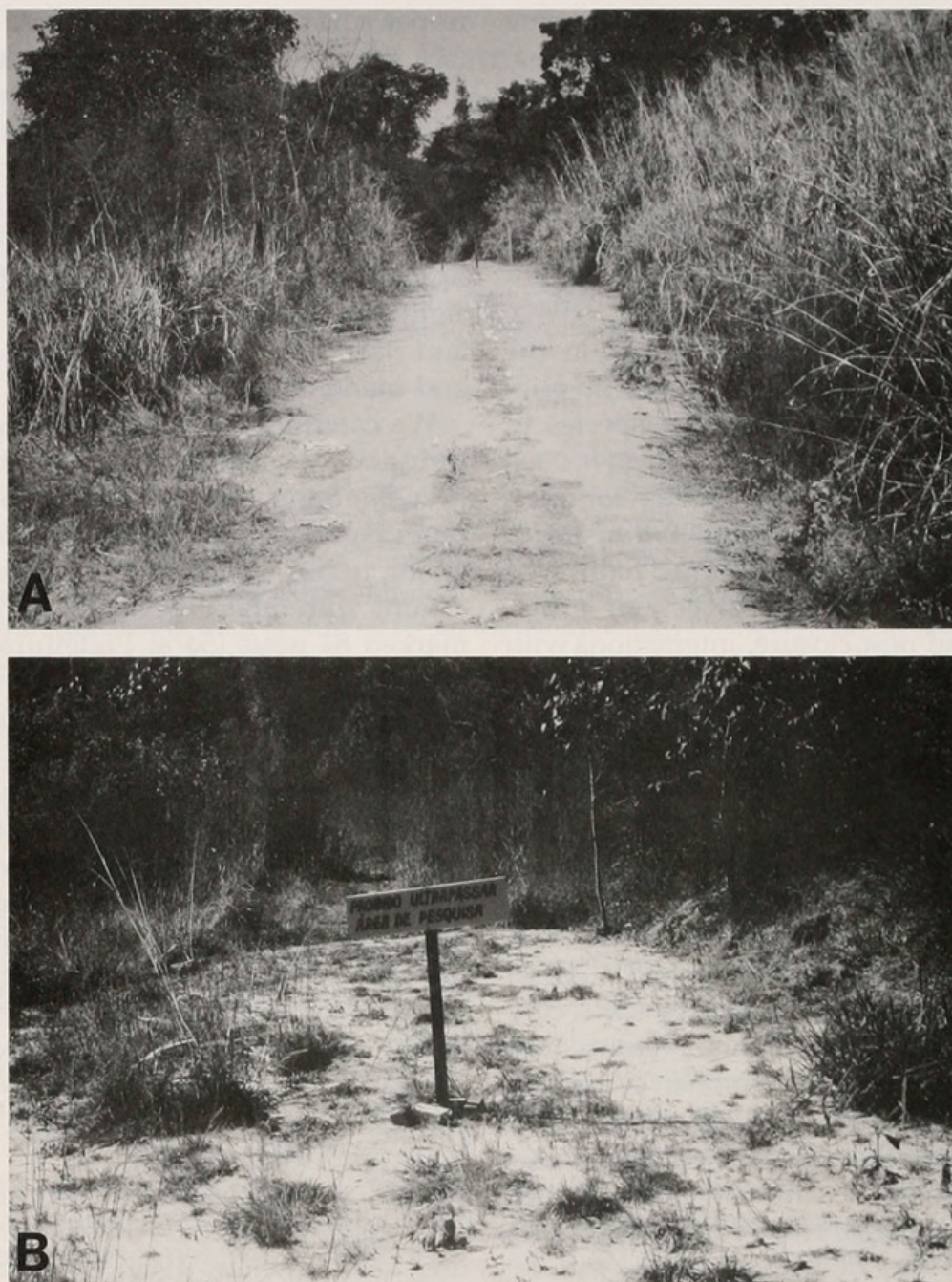


Fig. 1. A-B. Nesting sites, A. "Prefeitura," showing the homogeneous nature of the area, B. "Estação Ecológica," showing the heterogeneous, patchy nature of the area.

Metopia species (Diptera: Sarcophagidae: Miltogramminae) have been placed in the Swedish Museum of Natural History, Stockholm, Sweden. The nest distributions underwent nearest neighbor analyses in one dimension (after Boots and Getis 1988), using each nest as a point along a line. The nesting sites were linear in nature, and so were compressed longitudinally so as to be reduced to one dimen-

sional lines. To test whether our distributions were different from random, we calculated a *z*-value based on the *S*-statistic suggested by Durbin (1965) and compared it with the normal.

RESULTS AND DISCUSSION

The mean head width and thorax width of the marked *A. gracilis* was 3.33 ± 0.29 mm and 2.68 ± 0.25 mm, respectively

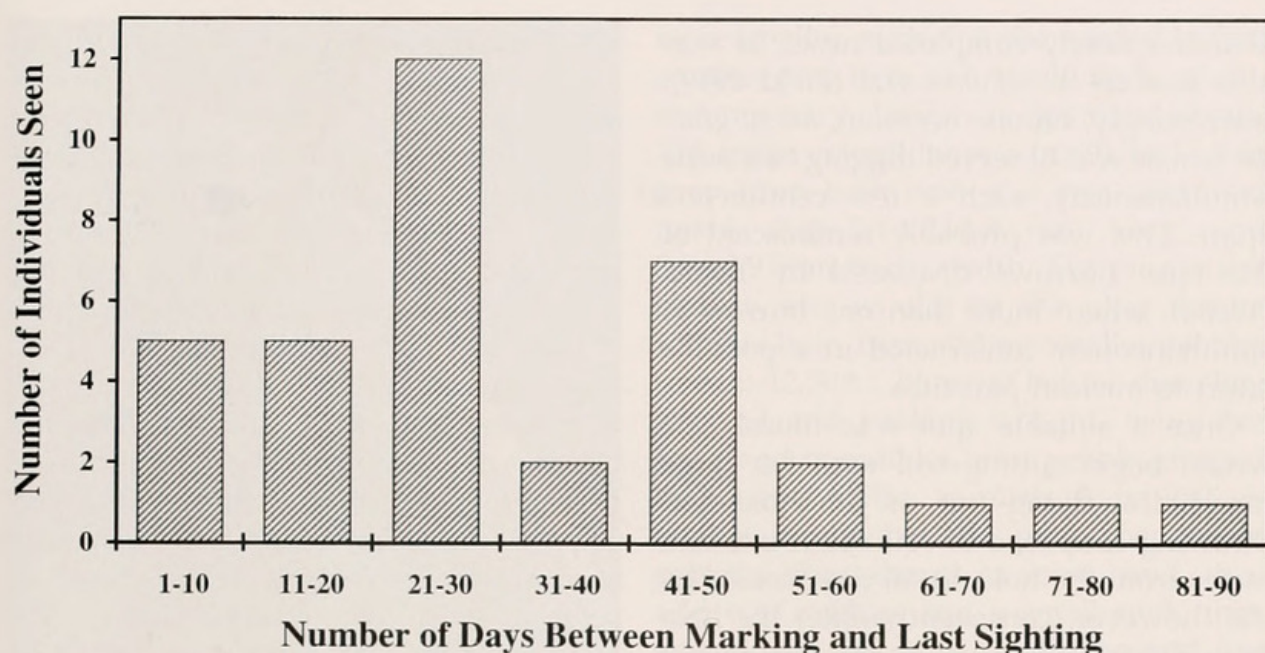


Fig. 2. Histogram representing the minimum longevities of the individual, marked *Ammophila gracilis* females.

($n=53$), with no differences between the sites.

Ammophila gracilis is a mass provisioner, always supplying 1 or 2 geometrid caterpillars (Lepidoptera: Geometridae) to a nest over a 1–2 day period before permanent closure. Other species are known to use a variety of prey, such as *A. aberti* Hal-deman, which prey on members of 14 genera in five families of Lepidoptera (Parker *et al.* 1980), and *A. harti*, which uses at least 16 genera in seven families (Hager and Kurczewski 1986).

Marked individuals were never observed far from where they were initially captured. At Prefeitura, individuals were only seen within about 10–20 m of their original marking site. At Estação Ecológica, they were never observed to move between clearings, and they were only seen in the same general area as they were originally marked in a given clearing. As in *A. harti* (Hager and Kurczewski 1986), marked *A. gracilis* females each constructed their own nests within this same area. However, each individual wasp was not seen every day, and their activity on those days is unknown, but of interest. The

wasps were typically active only during sunny periods of the day, with little or no activity on cloudy days.

The adult life span of *A. gracilis* is considerably longer than for any other *Ammophila* species recorded. The minimum longevity histogram (Fig. 2) represents the longest period of time between our initial marking and last sighting of an individual, with 84 days being the longest interval. Eighteen individuals were never seen after the initial marking (not shown in Fig. 2).

Nest Digging

The general nesting behavior was similar between the study sites. Typically, while searching, the female wasp would not act aggressively towards other insects. She usually concentrated her search in sandy patches and along cracks of more compact ground, and would often start digging in several different spots before finally settling in on one, similar to that of its close relative (another *Ammophilini*), *Podalonia robusta* (Cresson) (Kurczewski *et al.* 1992). On most occasions she would use pebbles and sand to rebury unsatisfactory holes, and would occasionally

abandon nearly completed nests, as was also seen in *A. sabulosa* (L.) (Field 1989). Interestingly, on one occasion, an *A. gracilis* female was observed digging two nests simultaneously, each a few centimeters apart. This was probably reminiscent of the false burrows discussed by Evans (1966a), where more than one burrow is simultaneously constructed in a possible effort to mislead parasites.

Once a suitable spot was found, she would begin cutting soil with her large mandibles, flying out of the hole and throwing each load of soil about one-half meter from the hole, in all directions. She did, however, consistently enter the hole from a single direction. As she dug deeper (to approximately thorax depth), she would start flying out of the hole in a single direction, about 45° to one side of her entrance direction, throwing soil farther from the hole each time, with a maximum distance of about 1.5–2.0 m. This behavior of flying loads of soil away from the nest was also reported, and nicely illustrated with photographs, for *A. pubescens* Courtis and other sphecids (Olberg 1959). Completed nests averaged 21.6 ± 2.0 mm deep, with an entrance diameter of 6.4 ± 0.8 mm ($n=18$).

During the entire process she would regularly stop and fly into the nearby vegetation to take nectar from any of several plant species, including *Elephantopus mollis* Humboldt, Bonpland, and Kunth (Asteraceae), *Vernonia polyanthes* (Sprengel) Lessing (Asteraceae), *Bredemeyera floribunda* Willdenow (Apocynaceae), *Mitricarpus hirtus* (L.) DeCandolle (Rubiaceae), *Waltheria indica* L. (Sterculiaceae), and a *Sida* sp. (Malvaceae). These share the characteristic of possessing small flowers.

Interactions With Other Insects

While digging, female *A. gracilis* often had encounters with other insects. An ant crossing her nest building area was responded to aggressively, by attacking and hovering above, nipping at the ant until it

left. She would often carry the ant into the air, dropping it a few cm away, as was also observed for *A. dysmica* (Rosenheim 1987). When she encountered a female conspecific, or another ground-nesting wasp, which were common to the area, she would attack it aggressively, driving it away in a similar fashion as with ants.

The case of perching satellite flies (Diptera: Sarcophagidae: Miltogramminae), was rather interesting, and warrants further investigation. When a fly or flies were perching near her nest, she would often stop nesting activities and freeze. This has been aptly described as "freeze-stops" in some other sphecids wasps (Alcock 1975; Spofford *et al.* 1986), and was mentioned for *A. harti* (Hager and Kurczewski 1985). The wasp would also crouch low to the ground with her legs spread wide, remaining in this position until the flies left. This is described here as "crouching" behavior. Sometimes, however, she would attack the parasites, temporarily driving them from her nesting area. Despite such efforts, parasitism of the nests was at least 8.3% by these flies.

Provisioning and Nest Closure

Once the nest was complete, she would search for a plug to form a temporary closure. In searching for a plug, she would pick up and manipulate numerous pebbles in her mandibles, often dropping them without trying them in the hole before finally finding a suitable one, which was also observed in *A. aberti* (Powell 1964). Then she would plug the hole and pile several (mean: 6.25 ± 1.50 ; $n=4$) more smaller pebbles on top, finally shoveling sand over the entrance. Once so plugged, she would fly off and disappear, usually not to return for over an hour or two, and sometimes not until the next day. On several occasions, we observed females moving to tall grass and running their mandibles up and down the blades, as if cleaning the mouthparts.

Eventually, she could be seen dragging,



Fig. 3. Egg of *Ammophila gracilis* on the first abdominal segments of the prey caterpillar.

or taking short hopping flights with, a paralyzed caterpillar, which she had grasped in her mandibles below its thorax, usually venter up, as has also been observed for several *Ammophila* species (Powell 1964; Tsuneki 1968). Then she would find her plugged hole, drop the caterpillar nearby, and unplug the nest. At both sites, ants would occasionally carry off the prey if left for more than a few minutes. Rosenheim (1989) observed that over 5% of prey items of *A. dysmica* were stolen by ants. After inspecting the nest, she would back down the hole, dragging the caterpillar down head first, and would remain inside for 1–3 minutes before exiting, presumably laying an egg on the lateral part of the first few segments of the prey's abdomen (Fig. 3), or on the second or third thoracic segment.

Then she searched out a new plug, or occasionally used the old one, to close the nest. If the first caterpillar was a large one (e.g., $2\times$ her own body size), she would put a permanent closure on the nest. If it

were smaller, such that she needed to find another prey item, she would make another temporary closure, as described above. The mean caterpillar size ($n=9$), including prey from both one- and two-caterpillar nests, was 30.4 ± 10.8 mm long, and 3.9 ± 0.9 mm body width. For permanent closure, she would set the plug deeper into the hole, then adding smaller pebbles (mean: 12.50 ± 1.29 ; $n=4$) before shoveling in sand and packing it tight, using her head and mandibles, or a pebble grasped in her mandibles, to push. A typical sequence would be: add plug, then seven pebbles, then shovel in some sand, then add two pebbles and a small stick, then shovel in some more sand, then add five pebbles, then finish by shoveling in sand. Once filled in with pebbles and sand, she would carefully camouflage the area by moving sand, pebbles, and small sticks around the entrance, even rearranging pebbles and sticks up to 0.5 m from the nest entrance.

Mortality and Emergence Patterns

Of those *A. gracilis* that emerged from both sites ($n=12$), the mean time period spent underground after nest closure was 56.30 ± 10.14 days. Although the range was quite wide (37 days), there was no correlation between days spent underground and the date. In fact, the individuals with the shortest (35 days) and longest (72 days) times were initially buried within four days of each other. An additional six pupae were excavated from their nests prior to adult emergence.

Of the remaining 66 nests that did not have *A. gracilis* emergence or pupae, seven nests were found to have been successfully parasitized by members of an undescribed species of *Metopia* (*Allenicia*) Townsend (near *M. sinipalpis* Allen) (Diptera: Sarcophagidae: Miltogramminae) (T. Pape, pers. comm.). Each of these nests produced from one to ten flies within 35.75 ± 4.99 days after nest closure. After excavation, some prey items were ob-

served to have up to 15 parasite eggs clustered over the caterpillar's head capsule or first thoracic segment. No other parasites were recovered from nests of *A. gracilis* in this study, although there were numerous digger wasp and bee parasites (especially Diptera: Bombyliidae, and Hymenoptera: Chrysididae, Mutillidae, and Leucospidae) present at each site. We can only speculate about the remaining mortality factors, which were responsible for the non-emergence of 59 of the 84 total nests. We suspect that there is extremely high ant predation, as all of these nests were excavated to yield no remains whatsoever. Rosenheim (1987) observed that ants would also prey on nest contents after final nest closure in *A. dysmica*. Therefore, we do not know the true rate of miltogrammine fly parasitism, as these nests could also have been removed by ants. Assuming nests with flies were destroyed by ants at the same rate as those with wasps, fly parasitism could have been as high as 28%.

On only one occasion did we observe the results (but not the event itself, unfortunately) of physical removal of a prey item after nest closure. Within one day after an observed final nest closure, we found the nest unplugged with the paralyzed caterpillar beside the entrance, with no *A. gracilis* egg attached. This removal of prey may have been by a conspecific, as has been observed, for example, in *A. sabulosa* (Field 1989), *A. dysmica* (Rosenheim 1987), and *A. aberti* (Parker *et al.* 1980).

Interestingly, the total mortality for *A. gracilis* was quite high compared to other published accounts of *Ammophila* species. The total mortality for both study sites was 78.6% (66 of 84 nests), with Prefeitura mortality at 72.3%, and Estação Ecológica mortality at 90%. Mortality rates for other species include: 52.5% for *A. dysmica* (Rosenheim 1987); 51.7% for *A. harti* (Hager and Kurczewski 1986); and 33% for *A. sabulosa* (Field 1989). Outside of *Ammophila*,

the mortality of another sphecid, *Tachysphex terminatus* (Smith), due to miltogrammine fly parasitism alone, was 30.6–57.9%, depending upon nesting site (Spofford *et al.* 1986). Only 10.6% of the mortality of *A. gracilis* could be explained by miltogrammine fly parasitism, although the actual rate of parasitism is probably considerably higher if ant predation of closed nests is great.

Nest Distributions

For our nearest neighbor analyses, using Durbin's S-statistic (Durbin 1965), we concluded that the distribution of *A. gracilis* nests was clumped at Prefeitura. The calculation of the S-statistic for the Prefeitura nests yielded a z-value of -2.406. Because this calculated value of z is negative and the value obtained from the tables of the normal distribution is smaller than 0.05 ($P=0.016$), the H_0 (that the distribution of nests is random) is rejected in favor of one indicating a clumped distribution of points along the line. Regarding the distribution of nests at Estação Ecológica (using only the most heavily nested clearing, at the beginning of the series of patchy clearings), we found that we could not reject H_0 . The calculation of the S-statistic yielded a z-value of -1.027. The value obtained from the tables of the normal distribution is larger than 0.05 ($P=0.306$), indicating the distribution cannot be considered different from random. This could possibly be explained by the smaller sample size, or it may be a real difference in the distributional patterns between the two sites.

If the differences in nest distributions between the sites are real, they can be accounted for. It is possible that there is a differential parasite and predator pressure, causing more clumping and aggregation at the Prefeitura site, but more data is needed to support this. If that is the case, there may be less pressure on *A. gracilis* in the very diverse, patchy areas of Estação Ecológica, where they could be

more difficult to find by searching, generalized parasites. Prefeitura is a very large, open, and homogeneous site, with numerous other ground-nesting wasps continuously present. This, coupled with the numerous parasites could pressure the wasps into small aggregations, affording them at least some protection by sheer numbers, as a type of "selfish herd" response (Hamilton 1971; Wcislo 1984), where the probability of nest parasitism decreases with increasing nest density. However, it has also been proposed that parasite pressure may act against the formation of nesting aggregations, and in favor of delayed nest provisioning (Rosenheim 1989) or progressive provisioning (Evans 1966b; Hager and Kurczewski 1985).

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