

**Nest parasitism and nest defense in the solitary ground-nesting wasp
Ammophila aberti Haldeman, 1852, with notes on the nesting behavior
of *Ammophila parkeri* Menke, 1964 and *Podalonia mexicana*
(de Saussure, 1867) (Hymenoptera: Sphecidae)**

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Abstract. *Ammophila aberti* Haldeman, 1852 is a solitary ground-nesting wasp that might be expected to be highly vulnerable to nest parasites, as it forms aggregations that can concentrate parasite foraging activity and provisions each nest with a series of small prey, necessitating repeated openings of the nest, each of which creates an opportunity for parasite entry. We studied a small population in which the nest parasite *Argochrysis armilla* Bohart, 1982 destroyed five of 15 provisioned nests (33%). But we inferred parasite oviposition in an additional third of nests (five of 15) that, nevertheless, successfully produced *A. aberti* offspring, with host wasps successfully defending invaded nests with an extended nest cleaning behavior. We also describe the basic nesting behavior of two additional species, *Ammophila parkeri* Menke, 1964 and *Podalonia mexicana* (de Saussure), 1867, both of which capture a single large caterpillar prey before excavating a nest.

Keywords. ground-nesting wasp, nest defense, nest parasites, subsocial behavior

INTRODUCTION

Eusociality in insects is a remarkable evolutionary innovation, and biologists have a longstanding interest in understanding the evolutionary pathway(s) through which sociality may have emerged. Evans & West-Eberhard (1970) proposed a highly influential hypothesis that sociality may have evolved through a progressive, incremental series of transitions (the “social ladder” model), the earliest stages of which involved an elaboration of parental care and extended parent-offspring contact in subsocial wasps. The genus *Ammophila* W. Kirby, 1798 figured prominently in the ideas of Evans & West-Eberhard (1970), as members of the genus exemplify several of the earliest extensions of parental care. More recently, Linksvayer & Johnson (2019) have cautioned against uncritical acceptance of the social ladder model and emphasized the need for tests based on explicit phylogenetic hypotheses. In a seminal paper that used a molecular phylogeny for the subfamily Ammophilinae and reconstruction of ancestral behavioral character states, Field et al. (2020) showed, perhaps surprisingly, that evolutionary transitions between different types of parental care are not unidirectional; their analysis documented multiple examples of transitions towards more abbreviated parental care.

Our long-term goal is to build upon the results of Field et al. (2020) in two ways. First, we seek to increase the density of taxon sampling by uncovering the parental care traits of a greater number of species in the genus *Ammophila* and near relatives, including *Podalonia* Spinola, 1853. Second, we seek to better understand the selective forces that might favor evolution of reduced parental care traits. This is a question that has received relatively little attention. Within the genus *Ammophila*, different strategies

of offspring provisioning may have various costs and benefits related to the efficiency of hunting and prey transport; the availability of prey of different sizes; and the robustness of different provisioning patterns given the uncertainty of parental longevity (Field 2005). Another factor that may differentially reward or penalize offspring provisioning traits are nest parasites. Whereas increased parental care is usually proposed to improve parental protection of offspring from natural enemies (Evans 1966, Field & Brace 2004, Field 2005), in the case of ground-nesting wasps the nest itself is a major refuge from enemies, and any opening of the nest by the mother wasp may create opportunities for parasite entry (e.g., Millena & Rosenheim 2022). Thus, perhaps paradoxically, it is possible that natural enemies could be important in favoring evolutionary transitions both towards and away from extended parental care, in different contexts. Quantitative estimates of the impact of parasites on *Ammophila* species are, however, available for few species, limiting opportunities for a formal comparative analysis of the relationship between parental care behavior and parasite impact.

The primary focus of the current study is the solitary, ground-nesting wasp *Ammophila aberti* Haldeman, 1852. Although several authors have described the basic nesting biology of this species (Williston 1892, Hicks 1932, Evans 1959, Powell 1964, Ponder 1976, Parker et al. 1980, Jiménez-Jiménez & Palacios-Cardiel 2008), no one has reported parasitism rates. There are several reasons to think that this species might be subject to elevated parasitism risk. First, the species forms characteristic aggregations of nesting females (Hicks 1932, Evans 1959, Powell 1964, Parker et al. 1980), which may concentrate parasite foraging activity and elevate risk (Rosenheim 1990). Second, at our study site in the White Mountains, California, *A. aberti* females build nests adjacent to a small aggregation of another wasp, *Ammophila pruinosa* Cresson, 1865 whose nests are known to be parasitized by *Argochrysis armilla* Bohart, 1982 (Hymenoptera: Chrysididae) (Rosenheim et al. 2025). *Ammophila aberti* females are likely to be easy for this parasite to detect; *A. armilla* locates nest digging females visually (Rosenheim 1987b). The study site is nearly devoid of vegetation, making the large *A. aberti* females (mean body length = 25 mm, Menke 2020) highly conspicuous. Third, *A. aberti* provisions its nests with many (~4–9) small to medium-sized caterpillars (Williston 1892, Hicks 1932, Evans 1959, Powell 1964, Ponder 1976, Parker et al. 1980, Jiménez-Jiménez & Palacios-Cardiel 2008), necessitating repeated visits to the nest, each of which could create an opportunity for parasite penetration of the nest. Fourth, there are no recorded effective defenses against chrysidid parasites expressed by *Ammophila* spp. wasps. Some chrysidid parasites appear to use chemical camouflage or chemical mimicry of their hosts to avoid detection (e.g., Castillo et al. 2022). Nevertheless, *Ammophila* spp. hosts do appear, in at least some cases, to be able to detect the presence of chrysidid parasites, responding by halting the provisioning of invaded nests (Rosenheim 2021) or through increased attempts at nest cleaning (Rosenheim 1987b). Whereas nest cleaning has been shown to be potentially effective in reducing the impact of miltogrammine fly parasites, which deposit live first-instar larvae into nests that can be expelled from nests by cleaning behaviors (Rosenheim 1987b, Spofford & Kurczewski 1992), nest cleaning has not been shown to be effective against *A. armilla*, which glues its eggs firmly to the caterpillar, the cell walls, or the cell ceiling (Rosenheim 1987a).

The goals of the current study were four-fold: (1) to estimate the parasitism rate of *A. aberti*; (2) to describe any possible anti-parasite defenses; (3) to describe some aspects of the nesting behavior of *A. aberti*, and in particular the nest closures

constructed, in a level of detail that will support future comparative analyses; and (4) to record briefly the nesting behavior and parental care traits of two additional species, *Ammophila parkeri* Menke, 1964 and *Podalonia mexicana* (de Saussure, 1867).

METHODS AND MATERIALS

Study Site of A. aberti. We studied interactions of *A. aberti* with its nest parasites from 10–24 June 2025 in Inyo County, California, U.S.A. alongside Cottonwood Creek in the White Mountains (elevation 1607 m, 37.46664° N, 117.92926° W). Females constructed nests directly on and adjacent to an ~80-m stretch of a sandy unpaved road; nesting activity at this small aggregation had been observed in 2023 and 2024. A belt of cottonwood (*Populus* sp., Salicaceae) and willow (*Salix* sp., Salicaceae) trees grew along the creek. A variety of shrubs, including *Psoralea polydenia* (Torr.) Rydb. (Fabaceae), *Artemisia tridentata* Nutt. (Asteraceae), *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird (Asteraceae), *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae), and *Salsola australis* R. Br. (Chenopodiaceae) grew in the surrounding dry desert habitat. Virtually all annual plants had died prior to our arrival, as 2025 was a very dry year.

Interactions of A. aberti with Nest Parasites. The study site was too large to maintain continuous observation of all nests, and our original goal was to identify a sample of nests that could be excavated to estimate the nest parasitism rate. We did, however, record intermittent observations at nests and more extensive observations for a series of nests located in the central part of the nest site. Nest locations were marked with nails driven into the ground and a wire flag for subsequent excavation. We observed oviposition behavior of two nest parasites: *A. armilla* and an unidentified miltogrammine fly. *Argochrysis armilla* females learn the location of nests relative to local landmarks and monitor discovered nests over a period of days to await the return of host females to the nest, when parasites attempt to penetrate the nests to oviposit (Rosenheim 1987a). Oviposition by *A. armilla* is recognizable, despite occurring out of sight in the subterranean nest, because individuals that oviposit rapidly fly away from the nest upon exiting the burrow instead of perching nearby to resume their nest monitoring; this rapid bolting from the nest is distinctive, and in extensive studies of interactions of *A. armilla* with another host wasp, *Ammophila dysmica* Menke, 1965, was found invariably to indicate that eggs had been laid in the cell and that the nest, if any occupants developed successfully, would yield parasite offspring (Rosenheim 1987b, 2021).

As described below, we observed that *A. aberti* sometimes appeared to detect that their nests had been invaded by *A. armilla* and to respond with greatly lengthened belowground stays in their nests during a succession of nest-cleaning trips. We measured the mean duration of these cleaning trips to compare two categories of *A. aberti* visits: (i) cleaning visits to nests where we had observed parasite oviposition but that our subsequent nest excavations revealed that the host offspring nevertheless survived (i.e., successfully defended nests), versus (ii) all other cleaning visits, including visits to nests that were subsequently defended, but which occurred prior to the parasite oviposition event that we witnessed.

Calculations and Measurements. We calculated the mean duration of nest cleaning trips associated with either nest provisioning or non-provisioning nest checks as ([total cleaning time] / [total number of cleaning trips]). We tested for a difference in mean cleaning trip duration for defended versus non-defended nests by fitting a linear mixed

effect (LME) model using the *lme4* package in R (Bates et al. 2025), using nestID as a random effect to account for possible non-independence of successive observations made at the same nest.

Nests were excavated on 23–24 June 2025 to record nest outcomes; all nest occupants were returned to the nest cell after inspection, so that all sampling was non-destructive.

Means are presented ± 1 SD throughout. When we measured the same behavioral element multiple times at a given nest (e.g., the length of time required to complete a nest provisioning), measurements were first averaged for a given nest and then averaged across nests.

Nesting Behavior of A. parkeri. We observed three female *A. parkeri* digging or provisioning nests in a desert scrub area with gravelly sand on 25 June 2025 adjacent to an inactive sand quarry ~1 km SE of downtown Bridgeport, California (38.25084° N, 119.21453° W). The site is dominated by the shrub *Purshia tridentata* (Pursh) DC. (Rosaceae), with the less abundant *A. tridentata* also present. There were very few flowering plants present.

Nesting Behavior of P. mexicana. We observed a single female *P. mexicana* digging and provisioning a nest on 22 June 2025 in a small sagebrush-dominated sloping field adjacent to Middle Creek in the White Mountains, Esmeralda County, Nevada (elevation 2538 m; 37.83161° N, 118.28657° W).

Photography. Photographs of host wasps and their parasites were taken with a Canon 80D camera with a 100–400-mm telephoto lens.

RESULTS

Nesting Behavior of A. aberti. The nesting behavior of *A. aberti* matched that described by previous authors. *Ammophila aberti* dug shallow, unicellular nests (83.0 ± 14.1 mm to the bottom of the cell floor ($n = 17$, range 60–105 mm)) in well-packed, bare, level ground, with excavated soil deposited in flights of highly variable length (0.15–6.0 m). Average time required to complete the nest excavation was 94.8 ± 17.9 min ($n = 5$, range: 69–113 min); in one case, digging was halted in the late afternoon (18:10 h) and resumed the following morning (10:47 h). Over the ensuing 1–3 days female wasps mass-provisioned each nest with a series of small to medium-sized caterpillars (Fig. 1) that they carried to the nest in flight. Females also visited their nests periodically without adding caterpillar provisions; during these ‘nest check’ visits the nest was opened, a series of cleaning trips performed, and the nest reclosed. Although caterpillar capture was never observed, all hunting females flew into the willow and cottonwood trees that grew along the creek when leaving the nest to hunt; the only time we saw female *A. aberti* active in the dry desert scrub habitat was when they were nectaring on *P. polydenius* or at their nests.

Temporary nest closures, which were placed on the nest any time the female departed to hunt or at the end of daily activity, were highly variable in their construction. One element was universal: the use of a single pebble to plug the nest burrow. This plug pebble was placed at varying depths from the soil surface, ranging from ~0–10 mm, and temporary closures varied substantially in what else was added. Some closures consisted of nothing more than the naked plug pebble. Females elaborated other closures by kicking dirt and small pebbles over the closure from within 1–2 cm from the nest; this kicked material generally made the nest closure indistinguishable from the



Figure 1. Female *Ammophila aberti* drawing a caterpillar into her nest.

surrounding soil surface. In cases where the soil surface lacked loose material, females sometimes bit the soil surface or uppermost walls of the nest burrow to dislodge soil that then dropped or was kicked over the nest closure. Still other females also picked up small pebbles from around the nest and added them to the closure, with or without dirt kicked over the closure. Temporary closures never involved any packing of the nest closure material by the female wasp, and they were generally completed rapidly (time from placement of plug to departure of female = 85.5 ± 28.0 sec) ($n = 9$; range 15–258 sec).

Only four final closures were observed; they involved four phases of behaviors. First, a pebble was used to plug the nest deep (>25 mm) in the burrow. Second, wasps cycled between adding pebbles to the closure, kicking sand into the nest from within 1–2 cm of the nest, and packing the closure, often while holding a pebble in their mandibles and emitting loud buzzes ('buzz-packing'). The pebbles used while buzz-packing were usually left in the closure but sometimes discarded. This continued until the burrow was filled to near the soil surface. Third, female wasps left the nest to search on foot for various organic objects, including sticks, leaf fragments, parts of flowers, and especially the fluffy pappus attached to cottonwood seeds, which were returned to the nest and buzz-packed into the closure (Fig. 2); 1–12 of these organic objects were added to the closure. Finally, females would walk 3–9 cm away from the nest in different directions while kicking sand behind them to complete the camouflaging of their nests. Final closures required from 13 to over 42 minutes to be completed.

Nest Parasitism and Host Defense. Nest excavations revealed that *A. armilla* was the sole successful nest parasite, exploiting 33% (five of 15) of the provisioned nests. Two nests were found to be empty; we never observed either of these nests to be provisioned. Despite substantial activity of miltogrammine flies in the nesting area, we found no fly puparia in any of the nests.



Figure 2. Female *Ammophila aberti* adding fiber- and thorn-bearing seeds to a final nest closure.

Remarkably, of the 10 nests that successfully yielded *A. aberti* cocoons, four had been oviposited into by *A. armilla* (three of the nests received eggs from two successive parasites) and one had likely received eggs or larvae of a miltogrammine fly. Thus, *A. aberti* appears to have a means of successfully defending nests even after oviposition by nest parasites.

Before describing events at the five defended nests, we will describe observations made at an *A. aberti* nest that was successfully parasitized by *A. armilla*. This nest was constructed in the morning; the female returned for a nest check (without a caterpillar) 40 minutes later; during the nest cleaning trips an *A. armilla* female entered the nest, remained below for 8 seconds, and then rapidly flew away from the site upon exiting, the signature of parasite oviposition. Our intermittent observations of the nest documented one subsequent provisioning, and the nest yielded *A. armilla* cocoons.

In contrast, in at least some nests *A. aberti* appears to have a means of removing or killing *A. armilla* eggs or perhaps larvae following parasite oviposition. Although nest cleaning trips are the most obvious expression of nest defense, the number of cleaning trips per provisioning or nest check visit did not differ between defended nests (8.9 ± 4.5) ($n = 5$; range 3.5–15.0) versus the other nests (9.4 ± 4.9) ($n = 5$, range 4.4–16). Instead, females that performed cleaning trips at defended nests remained below ground for extended periods (mean cleaning trip duration = 59.0 ± 29.5 sec, $n = 5$), more than twice the duration of cleaning trips observed at non-defended nests (22.9 ± 3.2 sec, $n = 5$; LME model, $t = 1.82$, $P = 0.034$; Fig. 3). In four of the six observed cases of defense following *A. armilla* oviposition, these extended below-ground stays by the *A. aberti* female began immediately following parasite oviposition: females remained below ground for 2.26, 2.62, and 3.22 minutes immediately following parasite oviposition in three cases where we recorded exact times. In the two

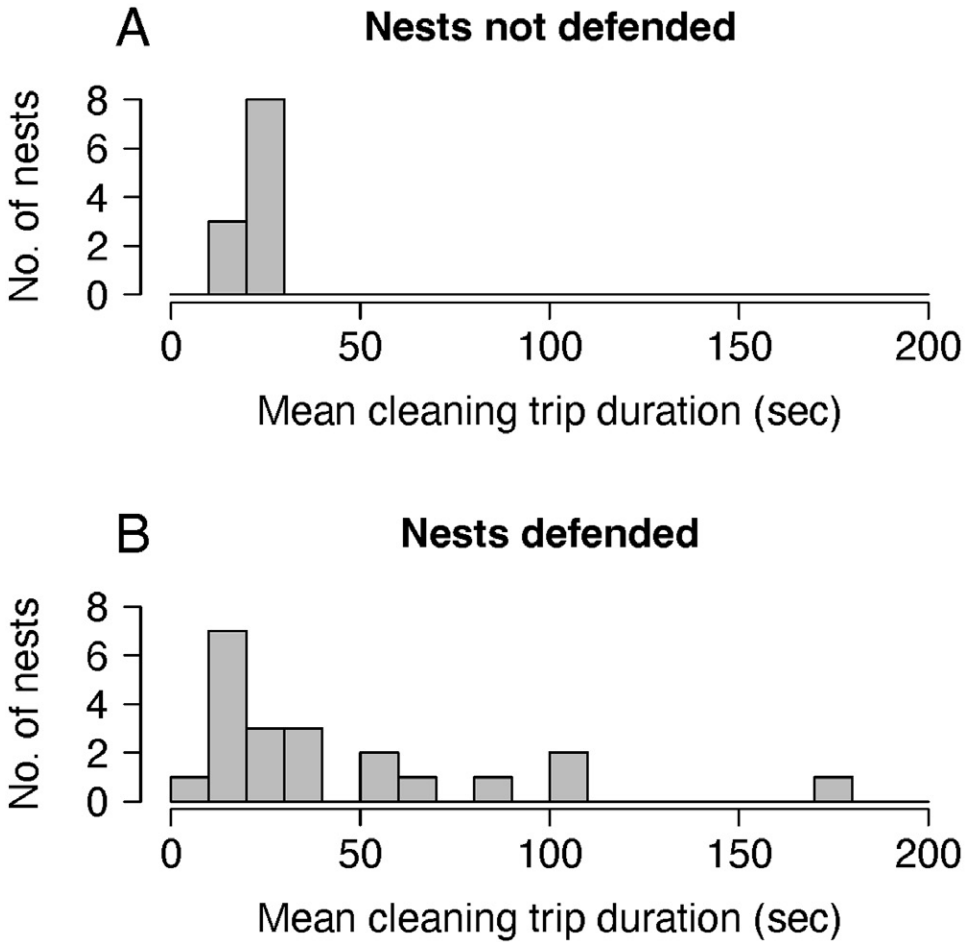


Figure 3. The mean duration per cleaning trip by *Ammophila aberti* females ($[= \text{total time cleaning the nest}] / [\text{total number of cleaning trips}]$) that are visiting nests, contrasting (A) nests that were not defended versus (B) nests that were defended. Defended nests are defined as those where behaviors associated with parasite oviposition had already been observed, but the nest nonetheless successfully produced *A. aberti* offspring.

cases of delayed responses, the long-duration belowground stays first appeared one or two days later, after at least three or seven nest visits for provisioning or nest checks, respectively. In one case only, the extended belowground stays by the host female were followed by the removal and discarding of three caterpillars from the nest; the nest was subsequently resealed and reprovisioned as a new nest (the first caterpillar added received a host egg, judging from the extended time associated with placing the first caterpillar), and yielded an *A. aberti* cocoon.

The fifth defended nest was invaded by a single unidentified miltogrammine fly (Diptera: Sarcophagidae). The fly entered the nest while the host female was cleaning the nest after a provisioning. The host wasp remained below ground in the nest for 3.00 minutes immediately after the fly exited the nest, and an additional provisioning of the nest was observed. We found only an *A. aberti* cocoon when the nest was excavated.

We do not know what the host wasps did below ground to defend their nests; these observations suggest, however, that *A. aberti* were able to destroy or remove the parasite eggs or larvae that had been deposited in their nests.

Nesting Behavior of A. parkeri. We observed three *A. parkeri* females that were either searching for a nest site, followed by excavating a nest, or in the midst of nest excavation; in each case, we observed the females to periodically visit a single paralyzed caterpillar that had been cached nearby in a plant, 3–12 cm off the ground. In each case, the female *A. parkeri* excavated a single-celled nest in which it placed the single caterpillar, laid an egg, and installed a permanent closure. Thus, *A. parkeri* captures its prey caterpillar before constructing a nest. All three observed females provisioned their nest with a single caterpillar of *Provia argentata* Barnes & McDunnough, 1910 (Lepidoptera: Noctuidae). This caterpillar is known as an herbivore of *Purshia glandulosa* Curran (<https://data.nhm.ac.uk/dataset/hosts>), and we suspect that it was feeding on the *P. tridentata* shrubs that dominated the site.

The study site had strikingly few nectar sources for *A. parkeri*. We found a single plant of *Tetradymia canescens* DC. (Asteraceae), a small shrub that was in abundant bloom, which was being visited by female *A. parkeri*.

During nest excavation, soil is removed in short (3–15-cm) flights. As we have observed for other species that dig the nest only after having captured a caterpillar, e.g., *Ammophila marshi* Menke, 1964 (unpublished data) and *Ammophila boharti* Menke 1964 (Rosenheim & Sandri 2023), nest digging is very rapid; two females each conducted eight cycles of digging and removing soil from the burrow in one minute. The females visited their cached caterpillars periodically while digging and repositioned their caterpillar closer to their nest as the digging progressed (Fig. 4).

The nest is closed without using a plug pebble. Instead, after pulling the caterpillar into the nest and ovipositing, females begin cycles of kicking loose dirt and tiny pebbles into the nest burrow from within 1–2 cm of the nest entrance and then entering the burrow to pack the dirt into place. The closure fills much of the nest burrow (females disappeared from view as they began the closure packing process). As the closure progresses, females also bit the surface of the soil around their nest entrance to loosen more material that could be kicked into the burrow. With rare exceptions, pebbles or other material were not carried into the burrow by the female using her mandibles; instead, everything was kicked in and then packed. The extensive biting of the soil surface eventually creates a 2–3-cm diameter disc around the nest entrance that is 2–3 mm below the surface area of the surrounding ground. This depressed disc is finally filled in by the wasp when it begins to walk in longer, 2–3-cm radii away from her nest, kicking loose sand and pebbles over the nest until the burrow location becomes indistinguishable from the surrounding soil surface.

Two nests were excavated; the single cells were 63 and 68 mm deep located at the bottom of straight, steeply sloping burrows. We observed male *A. armilla* watching host wasps during the digging and provisioning of the nests; hosts tried to chase these parasites away from the nest when they were detected. No parasites were observed to oviposit in the two nests where provisioning was seen, and no parasite eggs or larvae were detected in the two excavated nests.

Nesting behavior of P. mexicana. We observed only a single female, who was in the process of excavating a nest when we discovered her. She removed soil from the nest by backing out of the burrow while kicking sand behind her; this created a small tumulus—a flattened pile of sand behind the tunnel burrow. The nest burrow sloped



Figure 4. Female *Ammophila parkeri* re-caching a *Provia argentata* caterpillar on a small clump of grass.

down at a roughly 45° angle. Digging was very rapid, with the female backing out of the burrow kicking sand ~10 times per minute. After 25 minutes of digging, the female walked back to her caterpillar prey, a large noctuid cutworm (26 mm long, 5 mm wide) that she had previously cached 5 cm off the soil surface, ~0.8 m from her nest in a small clump of grass. She carried the caterpillar to her nest, drew it into the nest, remained below for 54 seconds, during which time she presumably oviposited, and then immediately began sealing the nest burrow. The female did not use a pebble to

plug the burrow; rather, she kicked dirt from the pile that had been deposited near the nest entrance into the burrow and then entered the nest, presumably to pack the dirt into place. As the soil of the tumulus was used up, the female started digging into the ground ~1 cm from the burrow entrance and kicking the loosened dirt into the original nest burrow. The burrow had been filled to nearly the soil surface when we captured the female for identification.

DISCUSSION

Parasitism of *A. aberti* nests by the chrysidid parasite *A. armilla* appears to be substantial, with 33% (five of 15) sampled nests being parasitized. However, it seems likely that parasitism rates could have been still higher were it not for what appears to be a successful anti-parasite defense: *A. aberti* performs an extended nest cleaning behavior in response to oviposition by nest parasites (both a miltogrammine fly and the wasp *A. armilla*) that, at least in our limited sample, consistently resulted in the *Ammophila* offspring developing successfully. Spofford & Kurczewski (1992) also listed “[i]nordinate amount of post-provisioning time in burrow (cleaning?)” as a possible defense against miltogrammine nest parasites by several genera of solitary sphecids wasps, including *Ammophila harti*, but without any further information about the behavior. Because we could not observe the host’s belowground behavior in nests during extended cleaning bouts, we can only speculate regarding the exact nature of the defense. We do not know if *A. aberti* is able to recognize and destroy parasite eggs or larvae following an extensive belowground search, or if a nonselective, comprehensive grooming of the lining of the cell allows the wasps to destroy or remove the parasites. Some bees have been shown to use nonselective grooming of provisioned pollen or the lining of cells as a defense against nest parasites (e.g., Torchio 1989).

When nesting females of the congener *A. dysmica* recognized nest parasites present during nest provisioning, they responded by doubling the number of cleaning trips they performed; these cleaning trips sometimes succeeded in removing larvae of parasitic miltogrammine flies from the nest, but they never succeeded in removing *A. armilla* eggs (Rosenheim 1987b). *Ammophila aberti*, in contrast, does not increase the number of cleaning trips in response to parasite detection, but instead lengthens their below-ground stays, deploying a defense that appears to be highly effective. Given the large number of provisioning visits required by *A. aberti* to provision a nest fully, and given the intense pressure from ovipositing nest parasites, it may be that this effective nest defense is necessary for *A. aberti* population persistence at this site.

Several questions are raised by our observations. If *A. aberti* has a highly effective nest defense, why doesn’t it use it more universally? Our observations suggest that the defense is only expressed conditionally, at nests where parasite oviposition is detected; perhaps failure to express the defense explains the 33% parasitism observed in our sample of nests. Alternatively, it may be that the lengthy nest defense behavior creates additional opportunities for parasites to oviposit, since the nest entrance is open during the cleaning process. Parasites that arrive at the nest late during the nest defense process might add eggs to an already ‘cleaned’ nest. We also don’t know how the host wasp detects the presence of parasites, including whether it is the adult parasite or the deposited eggs/larvae that are initially recognized. Additional work is needed to answer these questions.

Powell (1964) reported the only previous observation of *A. parkeri* nesting behavior, noting that it provisioned its nest with a very large caterpillar. Our observations establish that both *A. parkeri* and *P. mexicana* are species that capture a single caterpillar before digging a nest. These species join a growing list of *Ammophila* and *Podalonia* species for which this prey-nest sequence has been established (Rosenheim & Sandri 2023).

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