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Nesting behavior of the solitary ground-nesting wasp *Ammophila boharti* Menke, 1963 (Hymenoptera: Sphecidae)

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Abstract. Here we describe the nesting behavior of a previously unstudied solitary ground-nesting wasp, *Ammophila boharti* Menke, 1964. Species in the genus *Ammophila* are of particular interest because they exhibit a variety of parental care strategies. *Ammophila boharti* wasps were observed at two California field sites, one in the Mojave Desert and the other at the Antioch Dunes National Wildlife Refuge. *Ammophila boharti* begins its nesting cycle by hunting for a single, large caterpillar; all prey observed at Antioch Dunes were *Neoterpes ephelidaria* (Hulst, 1886) (Lepidoptera: Geometridae), which were feeding on California poppies, *Eschscholzia californica* Cham. (Papaveraceae). Female *A. boharti* wasps sting the caterpillar, inducing permanent paralysis, and then cache the prey off the soil surface on a plant while they excavate a shallow, unicellular nest. The caterpillar is then placed in the nest, a single egg laid on the caterpillar, and a permanent closure placed on the nest. No nest parasites were seen at any stage of the nesting process, and offspring within all excavated nests developed successfully through the larval stages to spin cocoons. Thus, this species exhibits a 'prey-nest' sequence of nesting behavior with almost no contact between the mother and her offspring, a minority condition within the genus.

Keywords. ground-nesting wasp, prey caching, prey-nest sequence, subsocial behavior

Introduction

Solitary ground-nesting wasps in the genus *Ammophila* W. Kirby, 1798 have long attracted the attention of researchers interested in the evolution of subsocial behavior, as the genus is speciose (Pulawski 2023), with 62 species known from North America (Menke 2020), and behaviorally diverse, including members with different degrees of extended parental care (Evans & West-Eberhard 1970). *Ammophila* species also exhibit remarkably intricate nest construction behavior and diverse strategies to defend their nests against a suite of nest parasites (e.g., Rosenheim 1987, Field & Brace 2004, Millena & Rosenheim 2022). Field et al. (2020) have recently used a molecular phylogeny to show that an early hypothesis that wasp behavior evolved through a regular series of unidirectional transitions towards greater parental care (the 'stepping stone' or 'social ladder' model for the evolution of subsociality (see Linksvayer & Johnson 2019)) is not supported; instead, behavioral transitions appear to be frequent in both directions, both towards and away from more extended parental care. To build upon the substantial progress achieved by Field et al. (2020), it is important to increase the number of species with known reproductive behavior that can be included in formal phylogenetic comparative analyses.

In this report, we describe the nesting behavior of a hitherto unstudied species, *Ammophila boharti* Menke, 1964, whose range includes California, Oregon, and Nevada, U.S.A., and Baja California and Chihuahua, Mexico (Menke 2020).

Methods and Materials

We observed the nesting behavior of *A. boharti* at two locations. First, on 16–17 May 1985 we observed two females constructing nests in the Antelope Valley of the

Mojave Desert near Littlerock, California in Little Rock Wash (34.5211, −118.0038). Little Rock Wash flows northward onto the floor of the Antelope Valley from the San Gabriel Mountains. Second, from 15–18 May 2023 we observed 11 females constructing nests at the Antioch Dunes National Wildlife Refuge in Antioch, California (38.0153, −121.7949), with supplementary observations made on 8 May and 2 June 2023. The location of each nest at the Antioch Dunes site was marked with a wire flag and a set of four numbered nails driven into the ground around the nest. Antioch Dunes National Wildlife Refuge is located along the southern bank of the San Joaquin River in the Delta Region of central California. It was historically a location with an extensive system of large sand dunes. Most of the sand was, however, mined in the early 1900s. The site presently has a sandy soil, some small, reconstructed dunes, scattered live oaks, and extensive grasslands harboring both introduced and native plants. We photographed nesting activity of *A. boharti* using a Canon 80D camera with a 100–400 mm telephoto lens. *Ammophila pruinosa* Cresson, 1865 was also present at low densities at various locations within the Antioch Dunes site but was not seen in the nesting aggregation where we observed *A. boharti* (females of the two species can be readily distinguished in the field). The nesting aggregation was located on and alongside an approximately 20-m stretch of a sandy road that was partially vegetated but also had some patches of open ground. Nine nests were excavated on 2 June 2023 to assess the developmental success of the provisioned offspring, and nest dimensions were measured with a hand-held ruler. Our description of nesting behavior is based on observations made at Antioch Dunes; supplementary observations made at the Little Rock Wash site are identified as such below. Summary statistics are reported throughout this report as the mean ± 1 SD.

Results

Nectar Sources. We observed male and female *A. boharti* nectaring on *Melilotus indicus* (L.) (Fabaceae), *Croton californicus* Müll. Arg. (Euphorbiaceae), and *Vicia villosa* Roth. (Fabaceae). Some *Ammophila* sp. wasps, most likely *A. boharti*, were also observed feeding on *Acmispon glaber* (Vogel) Brouillet (Fabaceae).

Male Behavior. Male *A. boharti* were observed throughout the day flying in low, sinuous paths along the road, likely in search of receptive females, and punctuated by visits to flowers for nectar consumption. Males chased each other, sometimes in tight, rising, spiraling flights, and landed momentarily on nesting females before resuming their search. We did not observe mating.

Nesting Behavior. The basic sequence in the nesting cycle of *A. boharti* is to search for a caterpillar prey; to sting and paralyze the caterpillar and cache it temporarily off the ground in a plant; to dig the nest; to transport the caterpillar to the nest, lay an egg, and seal the nest permanently. Each nest received only a single caterpillar, and we never saw a female return to a nest after it was provisioned and sealed.

Hunting. Females hunted for caterpillars under and on *Eschscholzia californica* Cham. (Papaveraceae) (California poppy) plants, which were common in the grassland areas immediately surrounding the nesting aggregation (Fig. 1); wasps observed in the Mojave Desert used a different, unidentified caterpillar of a species of Geometridae. Females walked rapidly on the ground under *E. californica* plants with occasional short hopping flights, their antennae touching the substrate, and making frequent turns to explore the soil surface and leaf litter. Periodically, the wasps flew upward into the plant,

Figure 1. *Ammophila boharti* female hunting on the foliage of a California poppy plant, *Eschscholzia californica*.

rapidly climbing along the plant stems with their tarsi in contact with the plant but with their upward progress assisted by their beating wings, tracing a path that moved straight upward until they reached the top of the plant—often with open flowers. If a caterpillar was not encountered, the female would then fly back to the ground to resume the ground-based search. We twice observed females encounter late-instar larvae of the geometrid moth *Neoterpes ephelidaria* (Hulst, 1886), which we infer was likely responsible for the widespread damage to *E. californica* flowers that we observed. In both cases, the caterpillar responded to initial contact with the wasp by dropping off the plant and falling to the ground. In response, the wasps flew quickly to the ground, relocated the caterpillars, and stung the thrashing caterpillars repeatedly (Fig. 2), rapidly inducing complete paralysis. All the caterpillars that we saw *A. boharti* use during 15 May–2 June 2023 for nest provisioning at Antioch Dunes appeared to be *N. ephelidaria*. Caterpillars were usually large relative to the body length of the female *A. boharti* (mean body length = 18 mm [Menke 2020]); we estimated mean caterpillar length relative to the length of the female wasp as 1.3 ± 0.3 wasp body lengths (range: 0.9–1.5; $N = 11$). On 2 June 2023, we observed a single *A. boharti* carrying a larger *N. ephelidaria* caterpillar approximately 2.0 times the body length of the female (Fig. 3). The geometrid caterpillars excavated from the two *A. boharti* nests in Little Rock wash were 33 and 42 mm in length. In all cases, each nest received just one caterpillar provision.

Prey Caching. Paralyzed caterpillars were carried by walking wasps up into a nearby herbaceous plant where they were hung over a plant structure for temporary storage (Fig. 4). In one case, a female remained on her newly cached prey and used her mandibles to repeatedly bite down on the caterpillar immediately behind the head capsule. We did not see any host hemolymph exuding from the host in response to these bites, and we did not observe the wasp to feed on the caterpillar. Wasps leaving

Figure 2. *Ammophila boharti* applying its stinger to the ventral side of a *Neoterpes ephelidaria* caterpillar that has just jumped off its host plant in an attempt to evade its predator.

Figure 3. *Ammophila boharti* female carrying a *Neoterpes ephelidaria* caterpillar, which is held with the mandibles and the forelegs.

Figure 4. *Ammophila boharti* female caching a paralyzed *Neoterpes ephelidaria* caterpillar in a plant.

their cached caterpillar prey performed a circular or oval flight around the cache site in which tighter looping flights were periodically superimposed on the larger, circular flight as the wasp progressed around the circumference of the circle or oval (Fig. 5); we interpret these flights as orientation movements during which wasps learned the location of the cache site relative to local landmarks.

Nest Site Searching. Wasps immediately initiated a nest-site search process following caterpillar caching. Wasps walked on the ground, biting the soil surface periodically, and often starting to dig and then almost immediately reject a site before resuming the search. Of the eight nesting females that we observed, two abandoned two successive nest sites after having excavated a tunnel that exceeded their body length; no late abandonments were observed at the remaining six nests for which some nest site searching was observed. Nests (N = 11) were sited in either essentially level ground (n = 6) or slightly to moderately sloping ground (n = 5), either in fully open, vegetation-free areas (n = 4) or under or near living or dead plants (n = 7) that cast only very partial shade on the digging site. The mean distance from the cached caterpillar prey to the site of nest construction was 3.1 ± 3.2 m (N = 7). Nest site searching required 5.2 and 28.7 minutes in the two cases where the initial capture and caching of the caterpillar was observed. Nest site search was often interrupted by quick visits to the cached caterpillar. Across all wasps observed, the time from our initial discovery of the nest-site searching wasp until the wasp's initiation of the nest that would eventually be completed was 34.1 ± 33.2 minutes (N = 8).

Nest Digging. Nest construction involved biting at the soil with the mandibles, gathering loosened sand into a packet held between the forelegs and the underside of the head, and disposing of the sand in short flights (ranging in length from 3-35 centimeters, and rarely farther) in various directions around the nest (Fig. 6). As digging progressed, all wasps were observed to perform looping orientation flights around

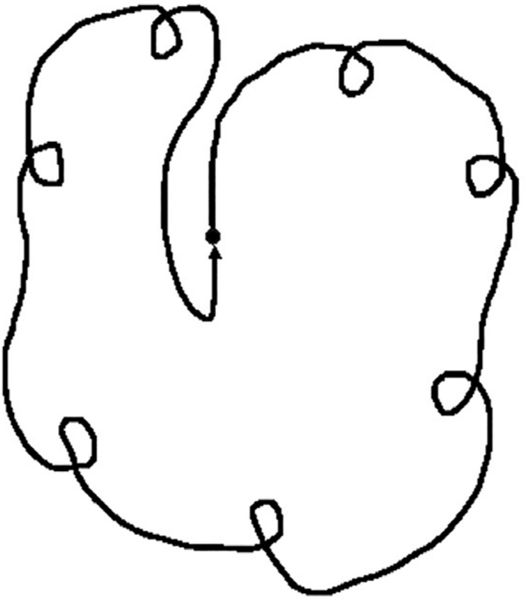

Figure 5. Typical form of an orientation flight by *Ammophila boharti*. Orientation flights were observed for females preparing to leave the site where they had cached a caterpillar prey or when excavating a new nest. These flights generally included a circular or oval overall shape, with a diameter of ca. 0.5–1.0 m, with much smaller superimposed loops executed while the wasp circled the nest or cache site.

Figure 6. *Ammophila boharti* female excavating a nest; a packet of sand is held between the forelegs and the underside of the head and discarded away from the nest in short flights.

Figure 7. *Ammophila boharti* female using its forelegs to kick a spray of sand behind it to complete the closure of its provisioned nest.

their nests, which were very similar in form to the orientation flights flown around caterpillar cache sites. Wasps sometimes interrupted their digging to make brief visits to their cached caterpillar, before returning to the nest to continue digging. The complete digging of a nest required an average of 52.4 ± 10.5 minutes (N = 7).

Re-caching of Prey. In six of ten nest diggings observed in their entirety, the wasp interrupted nest digging to return to the cached caterpillar and move it to a new location, closer to the nest under excavation, roughly mid-way through the nest digging (time from start of nest digging to re-caching of prey = 24.8 ± 7.7 minutes (N = 4); time from re-caching of prey to provisioning of nest = 19.3 ± 7.6 minutes, N = 5). Re-caching was seen in all cases where the original cache site was far from the site of nest digging (4.3, 4.6, and 9.1 m) but not where the digging site was close to the cache site (0.4, 0.6, 0.9, and 2.0 m). In five of six cases, new cache sites were very close to the digging site (0.10–0.76 m), but in one case the wasp moved the caterpillar from a very distant cache location (9.1 m from the nest) to one that was still 4.3 m from the nest. Caterpillars were cached 5.2 ± 2.8 cm (N = 10) off the soil surface. Re-caching of the caterpillar to a location closer to the nest was also seen for the one nest digging observed in full at Little Rock Wash.

Prey Transport and Nest Provisioning. Upon completing the excavation of the nest, wasps left the nest entrance open and flew to the cached caterpillar. The caterpillar was held with the wasp's mandibles and first pair of legs and carried head-first and venter up while walking back to the nest, where it was laid at the nest entrance. The wasp then pivoted 180 degrees, grabbed the caterpillar with its mandibles, and backed into the nest, pulling the caterpillar after it. Surprisingly, the wasp reappeared rapidly above ground (mean time to return from the cell = 19.4 ± 11.6 s, N = 10), which was presumably too rapid for the wasp to have oviposited. Wasps then performed a series (mean = 6.6 ± 3.1, N = 8) of cell-cleaning trips, removing sand and discarding it in

A

B

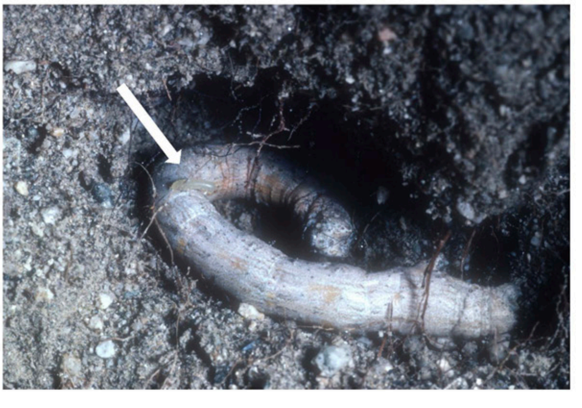

Figure 8. Cross-section of an *Ammophila boharti* nest excavated at Little Rock Wash. (A) Lateral view of entire nest; the white dotted line shows the contours of the soil surface, the nearly vertical nest tunnel, and the single cell containing a geometrid caterpillar; (B) a view of the caterpillar bearing an *A. boharti* egg (arrow), exposed by some additional excavation of the nest cell.

flight, before performing one final and relatively lengthy visit to the nest (mean duration = 58.4 ± 31.4 seconds; $N = 8$), from which the wasp emerged without any sand and immediately began sealing the nest. We hypothesize that this last visit to the nest was likely the occasion when the egg was laid.

Nest Closure. Wasps sealed their nests by executing four distinct phases of activity. (1) In the first phase, the wasp faced away from the nest and walked a very short distance (ca. 1–2 cm) while kicking sand behind her into the open nest tunnel, then returned to the nest tunnel to pack the loose sand into place with their heads. The characteristic use of a tunnel-plugging pebble that has been described for many *Ammophila* species was never observed. This sand kicking and tunnel packing behavior lasted for an average of 3.7 ± 1.2 minutes ($N = 7$). (2) The second phase of the nest closure began when the tunnel had been filled to a depth of approximately one body length of the female wasp (ca. 15–20 mm) and lasted for 1.8 ± 1.1 minutes ($N = 6$). It involved the wasp continuing to walk away from the nest a short distance (ca. 2 cm) while biting at the surface of the soil to loosen more dirt that was kicked back into the open tunnel, then rotating in a circular arc as if the tip of the wasp's abdomen were anchored above the open nest tunnel and the wasp's head was free to sweep in a circular motion around the nest. The wasp continued to bite the soil surface and kick dirt while performing these sweeping movements, which subtended different angles; sometimes approximately 90 degrees, sometimes 180, sometimes 270, and sometimes a full 360-degree circle. The result of this biting, kicking, and sweeping behavior was often a shallow circular trench dug approximately 4 cm in diameter entirely around the nest tunnel. (3) The third phase of the nest closure was typically initiated when the tunnel had been filled to within 5–10 mm of the soil surface and involved the wasp searching on foot for various objects, including clumps of dirt or dried plant parts, that were placed in the tunnel and then packed into place with the anterior surface of the wasp's head. Wasps made an average of 6.5 ± 2.4 ($N = 4$) trips to bring objects to the nest, requiring a total of 4.5 ± 4.4 minutes ($N = 5$). Often wasps appeared to return from these searching trips empty handed, having either failed to find a suitable object—despite picking up and immediately rejecting many candidate objects—or having dropped the selected object on the return trip to the nest. Pebbles were never used, perhaps because pebbles were largely absent from the nesting area. Females returning to nests with, or even without, objects sometimes also bit some loose sand off the edge of the tunnel entrance and packed the nest closure with their head. (4) During the fourth phase of the nest closure, which required 1.9 ± 0.6 minutes ($N = 5$), the female walked in straight vectors away from the now mostly filled nest entrance for longer distances (often up to 3–6 cm from the nest entrance) while continuously kicking sand behind her (Fig. 7). This had the effect of completely filling the nest tunnel and covering the circular trench created during the second phase of the nest closure. Wasps walked in different straight-line paths away from the nest while kicking loose sand to eliminate completely all visual traces of the nest closure. During this fourth and final phase of the nest closure, some, but not all, females also collected loose objects, such as dried plant debris, while walking away from the nest and returned to the location of the now hidden nest tunnel to deposit them there to further camouflage the location of the nest. Across all four behavioral phases, the nest closure required a total of 13.4 ± 4.3 minutes ($N = 8$).

Nest Parasites. We saw no nest parasites associated with any of the observed nests or with females transporting caterpillars to the nest. *Pogonomyrmex californicus* Buckley, 1867 ants are abundant at Antioch Dunes, and aggressive interactions between nesting *A. boharti* and foraging ants were noted in half (five of 10) of the observed nests. Female wasps hovered over ants and dipped down to administer quick bites, sometimes lifting the ants off the ground and rapidly dropping them a short distance away.

Nest Architecture. We excavated nests on 2 June 2023; two of the 11 nests could not be located, as foot traffic through the nesting area had disrupted the nest locations.

Each of the remaining nine nests harbored an *A. boharti* cocoon, indicating successful development from egg to prepupa, and no other nest occupants were found in the cells. The nest closure was found to involve filling the full length of the nest shaft with sand. Nest tunnels were 4.9 ± 0.2 mm in diameter (N = 10) and led at a steep downward angle to a single cell whose floor was located at a mean depth of 64.4 ± 8.5 mm (N = 9). The entrance to the cell was sometimes sharply angled from the path of the sloping burrow. Mean cell dimensions were: length, 15.6 ± 0.9 mm (N = 5); width, 8.5 ± 1.0 mm (N = 6); and height, 7.8 ± 0.5 mm (N = 5). Four of five nests whose cell floors were inspected also had a short, blind tunnel or 'well' in the middle of the cell floor, ca. 4 mm in diameter and 2–4 mm deep. Two nests excavated at Little Rock Wash had similar dimensions: tunnel diameter, 5.5 mm and 6.5 mm; depth to cell floor, 55 and 70 mm; cell length 31 mm; width 9 mm; and height 8 mm (Fig. 8). A well was also observed in one of the two nests excavated at Little Rock Wash.

Discussion

Ammophila boharti digs its nest only after first capturing, stinging, and temporarily caching its prey. Prey caching appears to be a means of reducing the likelihood that the caterpillar will be stolen by ants while the nest is being excavated (Rosenheim 1990). This prey-nest sequence has now been recorded in four North American *Ammophila* species: *Ammophila wrightii* (Cresson, 1868) (Hicks 1934), *Ammophila novita* (Fernald, 1934) (Ponder 1976, Alcock 1984), *Ammophila marshi* Menke, 1964 (J. A. Rosenheim, unpublished data), and *A. boharti* (this study), with all other studied species digging the nest before hunting for prey. Prey-nest sequences are found in many species in the closely related genus *Podalonia* Fernald, 1927 (Field et al. 2020).

Although we observed only a modest number of nests (N = 11) at the Antioch Dunes site, the complete absence of nest parasites was striking. Common nest parasites seen elsewhere in association with aggregations of nesting *Ammophila* species, including flies in the families Sarcophagidae and Bombyliidae and wasps in the family Chrysididae (e.g., Hager & Kurczewski 1986, Rosenheim 1987, Field & Brace 2004), were never observed in association with nesting females. Informal observations (ca. 20 wasps hand-netted and examined; a much larger number observed moving freely the field) also revealed no examples of parasitism by Strepsiptera. Thus, the Antioch Dunes population seemed to be operating largely free of the impact of common nest parasites, despite nesting at moderately high densities. Chrysidid (*Argochrysis* sp.) and strepsipteran parasites (*Paraxenos lugubris* [Pierce, 1908]) were observed to be common at Antioch Dunes during less intensive field sampling of multiple *Ammophila* spp. performed in the 1980s (J. A. Rosenheim, unpublished data).

Perhaps every *Ammophila* species has some distinctive behaviors expressed as part of their nest building strategies. For *A. boharti*, we observed three unusual traits. First, the form of orientation flights performed around the cache site and the nest site was unusual in that it included not just a circling flight around the site to be learned, but a large circular path onto which were superimposed smaller, tighter miniloops. This form of orientation flight has not, to our knowledge, been recorded previously. Second, *A. boharti* does not use a pebble or other relatively large object to plug the nest tunnel during the final closure. Pebbles were almost completely absent from the Antioch Dunes site, but the wasps observed in Little Rock Wash also closed the nest without the use of a plug pebble. Of the three other *Ammophila* species that capture a caterpillar before excavating a nest, two (*A. novita* and *A. marshi*) also do not use a pebble or large object to plug the burrow during final closure (Ponder 1976, J. A. Rosenheim, unpublished data), whereas *A. wrightii* does (Hicks 1934). Third, the spinning movement made by the wasp when biting the soil surface around the periphery of the nest during the nest closure also has not, to our knowledge, been recorded for any *Ammophila* species.

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