Nesting behavior of the progressively provisioning solitary ground-nesting wasp *Ammophila pruinosa* Cresson, 1965 (Hymenoptera: Sphecidae)

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Abstract. We describe the nesting behavior of a previously little studied solitary ground-nesting wasp, *Ammophila pruinosa* Cresson, 1965. Species in the genus *Ammophila* Kirby, 1798 are of particular interest because they exhibit a variety of parental care strategies. *Ammophila pruinosa* wasps were observed at a site in the White Mountains of California, U.S.A. Females of this species excavate shallow, unicellular nests, exhibiting progressive provisioning. In each nest, a single egg is laid on the first caterpillar provisioned, and after a pause of 3–4 days a series of additional caterpillars are added in an extended period of foraging before a final closure is placed on the nest. At least three nest parasites were recorded, with 4 of 11 nests being coopted by these parasites.

Keywords. ground-nesting wasp, progressive provisioning, subsocial behavior

Introduction

Solitary ground-nesting wasps in the genus *Ammophila* Kirby, 1798 have been studied as examples of how extended parental care strategies might evolve as precursors to eusociality (Evans & West-Eberhard 1970). The 'social ladder hypothesis' posits that more extensive contact between mother wasps and their offspring has evolved through a series of incremental and unidirectional behavioral transitions (Evans & West-Eberhard 1970, Linksvayer & Johnson 2019). Although intuitively appealing, this hypothesis has received few tests grounded in an explicit phylogenetic framework. A seminal study by Field et al. (2020) using data from the family Sphecidae suggested instead that behavioral transitions have occurred both towards and away from more extensive parent-offspring contact. Although extended parental care is often thought to enhance protection from natural enemies, in some cases parasites may penalize species with more extensive parent-offspring contacts, for example when the infectious stage of the parasite uses the mother wasp as a vector to reach the vulnerable wasp offspring within the nest (Millena & Rosenheim 2022).

To extend the insights generated by Field et al. (2020), we need to document the parental care behaviors of a greater array of sphecid wasp species, as most taxa remain unstudied. In this regard, *Ammophila* species that exhibit progressive provisioning are of particular interest. Under progressive provisioning, mothers bring provisions to their offspring gradually as they develop, creating an extended period of interactions between the mother and her larval offspring and allowing the mother to adjust provisioning decisions to the changing needs and health of the offspring (Field & Brace 2004, Field et al. 2025; see also Rosenheim 2021). Progressive provisioning has been viewed as the most derived and intimate form of parental care that has evolved within the genus *Ammophila* (Evans & West-Eberhard 1970). This can be contrasted with the more common 'mass provisioning' of offspring, under which all provisions are

brought to the nest in a single period of foraging, such that mother wasps generally complete nest provisioning before their offspring hatch from the egg. Progressive provisioning has been documented for only a handful of *Ammophila* species worldwide, including *Ammophila pubescens* Curtis, 1836 (Field & Brace 2004), *Ammophila azteca* Cameron, 1888 (Evans 1959), *Ammophila harti* (Fernald, 1931) (Hager & Kurczewski 1986), *Ammophila rubiginosa* Lepeletier de Saint Fargeau, 1845 (Weaving 1989), and perhaps *Ammophila varipes* Cresson, 1865 (Ponder 1976).

Previous observations of *Ammophila pruinosa* Cresson, 1965 suggest that these wasps are also progressive provisioners (Powell 1964, Ponder 1976). These observations were, however, mostly fragmentary, with nests observed only intermittently, making it difficult to produce a definitive description of the full cycle of nest construction and provisioning activities. Furthermore, it is difficult to place these observational data within a phylogenetic framework, because *A. pruinosa* is now viewed as a species complex, within which four species have been described, including *A. pruinosa*, *Ammophila nancy* Menke, 2007, *Ammophila californica* Menke, 1964, and *Ammophila linda* Menke, 2020, and with additional, still undescribed species thought to be present (Menke 2020). This growing recognition of species-level diversity within the *A. pruinosa* species complex makes it difficult to know with confidence the identities of the wasps observed by Powell (1964) and Ponder (1976).

Thus, the primary goals of this study were two-fold: (1) to conduct uninterrupted, multi-day observations of nesting females in the *A. pruinosa* species group to describe the full cycle of nest construction and provisioning; and (2) to link these observations to wasps identified with DNA sequencing to clarify their species-level identities.

Methods and Materials

We observed the nesting behavior of *A. pruinosa* from 9–19 June 2024 in Inyo County, California, U.S.A. alongside Cottonwood Creek, where the eastern slopes of the White Mountains meet the Great Basin Desert (37.46664° N, −117.92926° W, elevation 1607 m). The study site was an approximately 10×20-m area alongside a sandy road in an area that had been plowed and leveled many years ago but has since been recolonized by annual and perennial plants. Dominant plants at and immediately surrounding the study site included big sage brush, *Artemisia tridentata* Nutt. (Asteraceae); dotted dalea, *Psorothamnus polydenius* (Torr.) Rydb. (Fabaceae); rubber rabbitbrush, *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird (Asteraceae); fourwing saltbrush, *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae); Russian thistle, *Salsola australis* R. Br. (Chenopodiaceae); desert trumpet, *Eriogonum inflatum* Torr. & Frém. (Polygonaceae); Indian ricegrass, *Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth (Poaceae); cheatgrass, *Bromus tectorum* L.; pepperweed, *Lepidium* sp. (Poaceae); California evening primrose, *Oenothera californica* (S. Watson) S. Watson (Onagraceae); cushion Cryptantha, *Greeneocharis circumscissa* (Hook. & Arn.) Rydb. (Boraginaceae); white sweetclover, *Melilotus albus* Medik. (Fabaceae); and yellow beeplant, *Cleomella lutea* (Hook.) Roalson & J.C. Hall (Cleomaceae).

We collected several *Ammophila* species at this site during three visits, including *Ammophila aberti* Haldeman, 1852, which was relatively abundant and formed a small aggregation of nesting females adjacent to our study site where only *A. pruinosa* nested. Informal observations suggested that the main nest parasites associated with *A. pruinosa* were also associated with *A. aberti* nests. We conducted continuous focal

observations at five nests, watching them without interruption from the early stages of nest excavation through their final closure and supplementing these observations with intermittent observations at an additional 12 nests. Nests were marked with numbered flags and a set of four nails driven into the ground around the nest entrance. Photographs and video of nesting activity were taken with a Canon 80D camera with a 100–400 mm telephoto lens. All observed nests were excavated on 19–20 June 2024 to record nest dimensions and determine the nest outcomes. Nest parasites recovered from cells were reared in glass vials at room temperature in Martinez, California, to obtain adults for identification.

Wasp offspring found developing in successful nests, including feeding larvae and prepupae that had spun cocoons, were preserved in pure ethanol. To establish the species identity of wasp offspring, we extracted DNA and conducted reduced representation genome sequencing using targeted enrichment of ultra-conserved elements (UCE) (Ward & Blaimer 2022). DNA sequences were compared with (i) sequences from male *A. pruinosa* specimens collected at our study site and other sites in western North America that had been identified using diagnostic male genitalia characters (Menke 2020) and (ii) with sequences of related taxa in the *A. pruinosa* group, including *A. nancy*, *A. californica*, and *Ammophila hallelujah* Menke, 2020.

All *Ammophila* species that provision nests progressively also maintain multiple active nests simultaneously (Evans 1959, Hager & Kurczewski 1986, Weaving 1989, Field et al. 2025). To document the distribution of female activity across nests requires females to be marked individually; we opted not to do this, however, because marking requires females to be captured and handled, and we wanted to describe the nesting behavior of undisturbed females. We did, however, mark a single female wasp on 10 June that was excavating a nest at a site just outside our primary study area; fortuitously, this female subsequently excavated nests in our primary study area, allowing us to document an example of simultaneous activity at multiple nests. An offspring from this female was included in our sample of individuals for which DNA sequencing was conducted.

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.

Results

Identity of Observed Wasps. We extracted and sequenced DNA from the offspring collected from six of our focal nests; in a maximum likelihood tree, estimated with IQ-TREE 2 (Minh et al. 2020), each of these individuals fell together into a clade with previously collected adult male specimens identified as *A. pruinosa* based primarily on genitalic characters, including one male collected in Emery County, Utah, relatively close to the type locality for *A. pruinosa* (Colorado Territory) (PSW, unpublished data). This clade was separate from other sequenced species, including *A. californica* and *A. nancy*, which Menke (2020) identifies as members of the *A. pruinosa* species group. We tentatively conclude therefore that all observed individuals were conspecific and likely correspond to *A. pruinosa*.

Nectar Sources. There were no flowering plants immediately within the focal nesting area, so our observations of nectar foraging came from informal observations made

in the surrounding plant community. The dominant source of nectar for female *A. pruinosa* appeared to be *P. polydenius*. More limited observations of nectaring by *A. pruinosa* were also made on *E. inflatum* and *C. lutea*. Other *Ammophila* species were also found nectaring on *M. alba*.

Male Behavior. Male wasps were absent from the nesting area; we never saw male mating attempts directed at females engaged in nesting activities, and we never observed mating.

Overview of Nesting Behavior. The basic nesting cycle of *A. pruinosa* is to excavate a nest; provision the nest with a single caterpillar on which an egg is laid; wait 2–4 days; inspect the nest; conduct a second period of nest provisioning during which several caterpillars are added to the nest in rapid succession; and seal the nest permanently. During the 2–4 day pause in provisioning activity the female may excavate and provision other nests. Thus, this species is a progressive provisioner. We now describe elements of the nesting cycle in more detail.

Nest Site Searching. The nesting area was flat and very lightly vegetated. Females searching for a nest site interspersed slow walking, making frequent turns and tapping the soil with their antennae, with short hopping flights. These females often stopped to bite at the soil surface as they explored. A noteworthy pattern was that females chose to initiate nests in exposed, sunny microsites during the early morning (before 11:00 h) and late afternoon hours (after 17:00 h) but chose either partial or full shade when nesting during the hot midday hours (11:00–17:00 h). Although our sample size was small ($N = 8$ nests), this pattern was statistically supported (Fisher's exact test, $P = .014$). Full shade was very rare on the nesting site, but both females that initiated nests during the hottest mid-afternoon conditions (at 15:06 and 15:42) chose fully shaded microsites behind small but dense shrubs. These observations were made on hot days (peak temperatures = 35.6–38.3°C) with almost zero cloud cover. Informal observations made of females attempting to initiate nest excavation during the mid-afternoon in sunny locations revealed that these sites were subsequently abandoned.

Nest Digging. Females excavated nests by biting at the soil surface, gathering loosened soil and holding it between the underside of the head and the forelegs, and flying away from the nest in various directions to discard it in flight (Fig. 1). These flights were highly variable in length, with some females making short flights (~5–10 cm) and others making much longer flights (~50–200 cm). Nest excavation was a lengthy process, requiring 100.7 ± 4.0 minutes ($N = 4$) from nest initiation to completion. Of six nests whose excavation was observed from the very outset, three were started late in the afternoon, and digging was interrupted later (at 17:26, 17:44, and 18:52 h) and resumed the following morning; temporary closures were placed on the nest in two of these three nests (see below), with one left open. Nests initiated in the morning or midday were completed on the same day, but in each case a single, short pause in digging activity was observed (lasting 7.0, 7.1, or 10.0 minutes) for which a temporary closure was placed on the nest before the female left the nesting area. These pauses in nest excavation were observed after the female had been digging for an extended period (28, 42, and 44 minutes), leading us to speculate that the pauses were opportunities for females to forage for nectar.

Temporary Nest Closures. Females generally installed temporary nest closures during a pause in nest excavation; after completion of the nest excavation; after each nest provisioning except the last one; and after the nest inspection made prior to the second period of nest provisioning. Temporary nest closures generally took one of two forms:

Figure 1.   Female *A. pruinosa* removing dirt from a nest being excavated by holding a packet of dirt between the undersurface of her head and her forelegs. Female *A. pruinosa* body length ranges from 14–20 mm (Menke 2020).

(i) a single plug pebble placed at the soil surface (Fig. 2), or (ii) a single plug pebble placed at the soil surface, supplemented with a series of additional, much smaller pebbles, and then covered with sand kicked over the nest. The wasp active at one of our five continuously observed nests occasionally omitted the temporary nest closure entirely, leaving the nest open. Nest entrances sealed with only a plug pebble were still readily visible, as plug pebbles did not always create a very tight fit to the tunnel entrance. Nests sealed with multiple pebbles and sand were invisible to human observers.

The behavior of females kicking sand over their nest's entrance was distinctive: wasps made many short (2–3 cm) walks away from the nest, but each radial path away from the nest entrance was a sequence of segments (often ~10–12) that alternated slightly (~30°) to the left and then to the right. We called these distinctive movements 'zigzag walks.' Females kicking sand behind them over the nest curled their fore-tarsi into a U-shape, applying the outer margin of their tarsal segments, which bear stout, elongated setae, to the soil surface in rapid brushing motions (Fig. 3). These movements were too rapid to be seen with the naked eye, but they were revealed by our photography.

Individual females used both types of temporary closures. Females consistently installed the more extensive closures, including extra pebbles and sand, before lengthier stays away from the nest: after the initial nest provisioning and oviposition ($N = 7$) and before overnight interruptions within the second period of nest provisionings ($N = 3$). Three of the five continuously observed nests also showed occasional examples of more extensive temporary nest closures following the placement of caterpillars in nests during the second period of provisionings.

Orientation Flights. Females made slow flights around their nests that we interpreted as orientation flights, during which females learn the locations of their nests relative to

Figure 2. Female *A. pruinosa* carrying a pebble to the nest that will be used to plug the surface of the nest tunnel during a temporary nest closure.
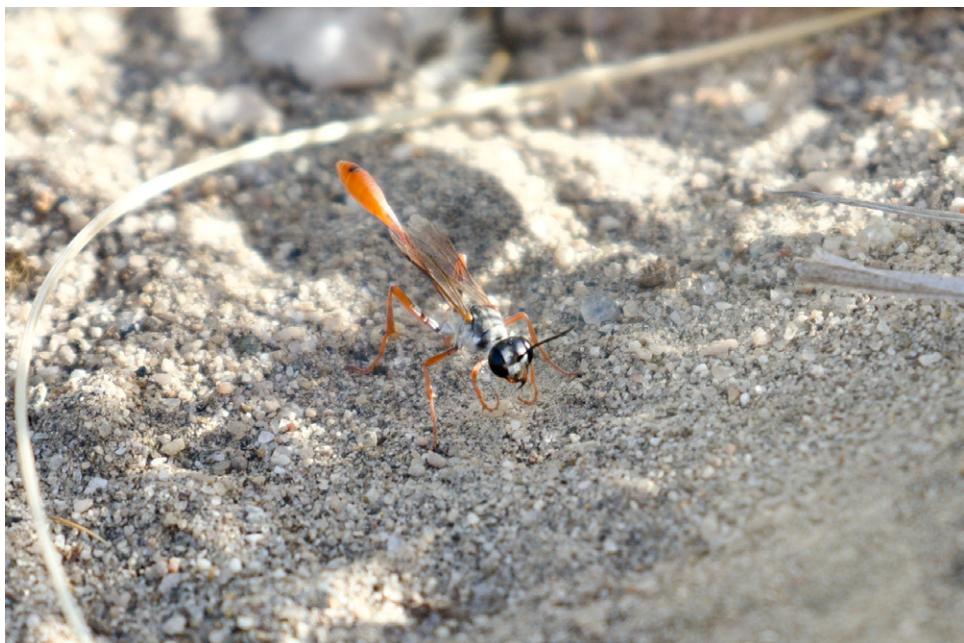

Figure 3. Female *A. pruinosa* kicking sand behind her over her nest by curling her fore-tarsi into a U-shape. This allows the female to rake the stout, elongated setae that are found on the outer edges of her tarsi against the soil surface.

local landmarks. However, unlike many other *Ammophila* species, the form of the orientation flights for *A. pruinosa* females was not highly stereotyped. Orientation flights generally involved slow, roughly circling flights around the nest of increasing diameters, sometimes extending to distances of just ~1 m but other times to as far as 3–4 m from the nest. But the flights sometimes included smaller loops, or side-to-side casting flights, or sometimes periodic landings on any slightly elevated soil surface feature. Orientation flights were observed during nest excavation; prior to any pause in nest excavation that was associated with the placement of a temporary nest closure; upon the completion of nest excavation; after the first provisioning of the nest; and after the nest inspection that occurs prior to the second period of nest provisioning.

Hunting and Prey Transport. Ammophila pruinosa females provisioned their nests with a wide array of small (typically between 0.4–1.0 times the body length of the female wasp) lepidopteran caterpillars, among which various species of the families Geometridae and Lycaenidae predominated. Hunting was observed on the foliage and stems of *P. polydenius*, *A. canescens*, and *B. tectorum*. Hunting was also observed on the ground below these plants; we made minimal effort to observe hunting wasps, however, so we suspect this is far from a complete list of host plants. The moment of prey capture was not observed, but one female was photographed first hunting on *B. tectorum*, then clutching a lycaenid caterpillar (Fig. 4), and then stinging the caterpillar (Fig. 5). Paralyzed caterpillars were generally transported in flight; in only one case was the caterpillar carried on foot and in very short (< 10 cm), hopping flights because it was too heavy for aerial transport.

First Provisioning. Nests received their first caterpillar provision soon after the completion of nest excavation; the mean time between the completion of digging and the

Figure 4. Female *A. pruinosa* clutching a lycaenid caterpillar that had just been captured on a seedhead of *B. tectorum*.

Figure 5.　Female *A. pruinosa* applying her stinger to the ventral surface of a lycaenid caterpillar that had just been captured on a seedhead of *B. tectorum*.

return of the female wasp with the first paralyzed caterpillar was 55.2 ± 40.7 minutes (range 11.8–130.2 min, $N = 7$). This is a much longer time than required for hunting during the second period of provisionings (see below), and thus we suspect that much of this time was spent nectaring or otherwise resting following the extended period of nest excavation. A female returning to the nest with her first caterpillar placed the caterpillar on the ground at the lip of the nest, rapidly removed the nest closure without entering the nest, spun around above ground, seized the caterpillar with her mandibles, and then backed into the nest, drawing the caterpillar in behind her (Fig. 6). Females remained below ground with this first caterpillar provision for an average of 62.0 ± 12.9 sec ($N = 6$); we interpret this largely as the time required to lay an egg, as the time required to stow subsequent caterpillar provisions was much shorter (see below). Females then emerged from the nest head-first and without carrying any sand, re-entered the nest to perform a series of cleaning trips (mean number = 4.2 ± 1.6, $N = 6$), discarding sand in short flights, and then placed a temporary closure on the nest. The total time at the nest for the first provisioning was 5.3 ± 1.0 min ($N = 6$).

Inspection Visit. There was a long pause in activity at the nests following the first provisioning. Assuming a roughly 10-h day of wasp activity (from ∼08:30–18:30 h daily), the pause between the first provisioning and the resumption of activity at the nest averaged 35.6 ± 7.0 h (range 23.7–41.3 h, $N = 5$). The resumption of activity at the nest was always signaled by a single nest inspection. For the nest inspection the female removed the nest closure, conducted a series of cleaning trips (mean number = 5.4 ± 2.7, $N = 5$), discarding sand in short flights, and replaced a temporary closure on the nest; the whole inspection visit required an average of 3.3 ± 1.9 minutes ($N = 5$).

Second Period of Provisionings. The inspection visit was, in all cases, followed by a rapid succession of nest provisioning visits. Wasps returned to their nests with

Figure 6.   Female *A. pruinosa* carrying a lycaenid caterpillar as she backs into the nest, having just removed the temporary closure.

caterpillars, rapidly removed the nest closure, sometimes conducted cleaning trips (mean number = 0.54 ± 0.50, $N = 5$), stowed the caterpillar in the nest (time below ground = 13.4 ± 4.1 sec, $N = 5$), conducted additional cleaning trips (mean number = 2.9 ± 2.9, $N = 5$), and finally replaced the nest closure. These provisioning visits were very rapid, requiring on average just 1.67 ± 1.27 min ($N = 5$). Females required an average of only 19.0 ± 5.3 min ($N = 5$) to hunt for, sting, and transport these caterpillars to their nests. We did not always detect that a focal female had returned to her nest soon enough to see the caterpillar before it was pulled into the nest, even if we inferred a nest provisioning by seeing the wasp cleaning and re-sealing the nest. In all, we saw or inferred females adding an average of 11.4 ± 4.4 caterpillars to the nest during the second period of provisionings (range 6–17, $N = 5$), actually seeing the caterpillars in 89.5% of these provisionings. Females required an average of 5.49 ± 0.91 h ($N = 6$) to complete the entire second period of nest provisionings.

Permanent Nest Closure. Upon completing the nest provisioning, females permanently closed the nest. The permanent nest closure most obviously differed from the temporary closures by the plug pebble being placed deep in the tunnel burrow; nest excavations (see below) showed that the plug pebbles were placed at an average depth of 30.5 ± 13.1 mm (range 5–50 mm, N = 11). In the one case of a shallow closure (plug at 5 mm depth), the female was seen struggling unsuccessfully to move the plug deeper, buzzing loudly while trying to push the pebble down. Upon placing the plug pebble, females then began adding a large number of small pebbles, gathered from the soil surface around the nest, and sometimes out to a distance of 1–2 m if pebbles were not readily located nearer. Females searched for pebbles on foot, seized pebbles in their mandibles, and rapidly flew to the lip of the nest in a single hop-like flight.

Most pebbles were simply dropped into the nest from the lip of the burrow, but females also rapidly entered nests to deposit some pebbles, immediately reemerging to search for additional pebbles. Females occasionally kicked a minimal amount of sand into the nest closure during the period of adding pebbles. Females were not observed to pack the contents of the filled burrow with their heads while buzzing, as has been reported for other *Ammophila* species (Hager & Kurczewski 1986, Rosenheim 1987b). The result was that the tunnel burrow was filled with a loose jumble of tiny pebbles (Fig. 7). As the pebble fill of the tunnel approached to within ~0–2 mm of the soil surface, the females transitioned to more extensive zigzag walking while kicking sand over the nest entrance, eventually completely covering the nest entrance. Finally, females often further concealed the sealed burrow by placing loose material from the soil surface (e.g., pebbles, grass seeds or small sticks) over the nest entrance. The entire process of adding the final caterpillar provision and installing the final nest closure required an average of 15.3 ± 7.8 minutes ($N = 6$). No wasps were observed to enter the nests after the final closure was installed.

Nest Parasites. We observed four common parasites foraging in the focal study area where *A. pruinosa* was nesting and in the adjacent *A. aberti* nesting area. These included two chrysidid parasites, *Argochrysis armilla* Bohart, 1982 and an unidentified larger species (inspection of photographs suggested a species of *Ceratochrysis* Cooper 1952), an unidentified miltogrammine fly, and an unidentified bombyliid fly. The chrysidids and the miltogrammine fly were observed to perch around *A. pruinosa* nests watching active females, whereas the bombyliid was active some days ovipositing in any visible burrow entrance (many other wasps and bees were nesting at the site) and sometimes near the base of grass clumps. Both chrysidid species were also observed to perform tight spiraling flights around *A. pruinosa* nests just prior to departing, suggesting that they might be learning the location of nests. Both species were also observed to visit nests in the absence of the nesting host wasps, landing on the nest closures or perching around the nests facing the nest closures.

On two occasions we observed what appeared to be cases of parasites penetrating *A. pruinosa* nests to oviposit. In one case, an *A. armilla* female was monitoring a nest when the host wasp returned to add the nest's second caterpillar provision; the parasite waited until the host wasp had placed the caterpillar in the nest and was searching for a plug pebble and then flew to the lip of the nest and ran down into the nest. The host wasp then placed a tight-fitting plug pebble, with the parasite still below in the nest; the parasite remained within the nest until the host wasp returned 16 minutes later with the nest's third caterpillar provision. The parasite rapidly flew out of the nest and away from the immediate location of the nest when the host wasp was removing sand in a post-provisioning cleaning trip. The host wasp did not exhibit any awareness of the parasite's presence and added an additional 12 caterpillars to the nest over the next several hours. Upon excavation, the nest contained only a cluster of *A. armilla* cocoons, covered with a hard coating of dirt and other debris from the cell. A second nest that was in the second period of nest provisioning received a plug pebble that was loose fitting; the larger chrysidid parasite entered the nest, apparently moving past the plug pebble; we did not see it exit the nest (this was not one of our focal nests). The nest received at least an additional three caterpillar provisions. Upon excavation, the nest contained a single, large, naked chrysidid cocoon surrounded by abundant loose silk threads that filled the cell.

Of 11 completed *A. pruinosa* nests that we excavated, seven contained healthy *Ammophila* larvae or cocooned prepupae; two contained only groups of *A. armilla*

Figure 7. A partially excavated *A. pruinosa* nest showing the loose jumble of pebbles that fills the upper portion of the nearly vertical tunnel shaft (approximate diameter of tunnel shaft = 4.0 mm).

cocoons; one contained a cocoon of the larger chrysidid parasite; and one contained both a single miltogrammine puparium and a pair of *A. armilla* cocoons. Because bombyliid parasites often develop on host wasp prepupae in their cocoons, and because we sacrificed all host prepupae for molecular host identification, we cannot assess bombyliid parasitism here.

Potential Predators. Nesting females often fought with ants of a species in the genus *Pogonomyrmex* Mayr, 1868, with wasps hovering over ants, dipping down to

administer quick bites, and sometimes carrying the ants away from their nests in very short flights (< 10 cm). We never saw the ants successfully attack female wasps or steal nest provisions. Western whiptail lizards, *Aspidoscelis tigris* (Baird & Girard, 1852), foraged frequently across the nesting area; in one case, we saw a whiptail attempt to bite a nesting female *A. pruinosa*; the attack was unsuccessful, and the wasp flew from the attack site. One unsuccessful attack was also seen by an unidentified robber fly (family Asilidae).

Nest Architecture. Excavated nests had a simple architecture, with a nearly vertical tunnel (diameter = 4.0 ± 0.1 mm, *N* = 13) leading to a single horizontal cell (length = 15.3 ± 1.9 mm, *N* = 9; width = 8.6 ± 0.9 mm, *N* = 12; height = 8.8 ± 1.6 mm, *N* = 9) at a depth of 73.1 ± 9.6 mm (range 55–93 mm, *N* = 13) (Fig. 8).

Multiple Active Nests. We marked only a single female at our study site. This female was active simultaneously at four widely spaced nests (nests at least 1.7 m apart) that were dug and given their initial provisioning during two days (10–11 June). We observed, at least intermittently, the second set of provisionings for three of these four nests (14–16 June); the fourth nest was outside our primary study site. On 14 June we also saw this female begin, and then abandon, excavation of a fifth nest.

Discussion

Our observations show that *A. pruinosa* provisions its nests progressively, with the female excavating a nest, immediately provisioning it with a single caterpillar upon which she oviposits, and then waiting 2–4 days before resuming provisioning of the nest, which by then is expected to contain a feeding larva. Our observations of a single marked female are consistent with the hypothesis that, like all other progressively provisioning *Ammophila* species studied to date, females are active at other nests during the 2–4 day pause in provisioning.

The studied population is attacked by several nest parasites. One of these, *A. armilla*, is a cleptoparasite that feeds indiscriminately on either the provisioned caterpillars or the developing *Ammophila* larva (Rosenheim 1987a). The second chrysidid appeared to be a *Ceratochrysis* sp.; one previous record of this genus attacking an unidentified species of *Ammophila* has been recorded (Kimsey 2014), but details of the parasite's development are unknown.

Powell (1964) and Ponder (1976) have described the nesting behavior of members of the *A. pruinosa* species group, and we can compare our observations with their published reports. Although the wasps we observed may provision their nests with a larger mean number of caterpillars (12.4 ± 4.4 in our sample of 5 nests, compared to 6–7 in nests examined by Powell (1964) and Ponder (1976)), in broad terms, our observations are concordant with these earlier descriptions: in all cases, wasps provisioned their nests progressively, with an initial nest provisioning followed by a multi-day pause and a second set of provisionings. Powell's (1964) description of the nesting behavior of what he called "*Ammophila* sp. near *pruinosa* (Species "1b" of Menke)" conducted at Antioch, California is fully congruent with our observations: he recorded temporary and final closures similar to what we observed, pebbles were often dropped into nest closures, and females did not pack their closures. These observations were very fragmentary, however, so it is hard to conclude confidently that there is a comprehensive match of behavior. We sequenced a female *Ammophila* that we collected at Antioch Dunes in 2021; it clustered tightly with the *A. pruinosa* that we sequenced from Cottonwood Creek.

Figure 8. A fully excavated *A. pruinosa* nest (same nest as shown in Fig. 7), showing the nearly vertical tunnel shaft (approximate diameter = 4.0 mm) and the single cell, in this case nearly filled by an *A. pruinosa* cocoon.

A close reading reveals some clear differences between our observations and those recorded by Powell (1964) for the Antioch population and both populations studied by Ponder (1976). We consider the most distinctive aspects of the nesting behavior of the Cottonwood Creek population of *A. pruinosa* to be the following: (i) temporary closures are very shallow, and are often just a single plug pebble at the nest surface; (ii) sand is added to closures through the zigzag walks, which have, to our knowledge,

never be described previously for any *Ammophila* species; (iii) during the final closure, the tunnel is filled almost exclusively with pebbles that are often dropped into the nest without the female entering; and (iv) the female does not engage in firmly packing the final nest closure at any stage; females of most *Ammophila* species use their flight muscles to vibrate their bodies as they press their head against the closure to create a tight pack ('buzz-packing;' e.g., Rosenheim 1987b). Some species hold a pebble in their mandibles during this behavior ('tool use') while others do not; but a firming of the nest closure is a feature of the final nest closure of most *Ammophila* species. Neither Powell (1964) nor Ponder (1976) provide a sufficiently detailed description of the sand kicking behavior of the wasps they observed for us to determine if their populations expressed the zigzag walks. Powell (1964) also observed a population of *A. pruinosa* species group wasps near Blythe, California; these wasps constructed nest closures very similar to what we observed but did not drop pebbles into nest closures and exhibited buzz-packing during the final closure. Ponder's 'population 1' constructed temporary nest closures with plug pebbles placed relatively deep (0.5–1.5 cm below the soil surface) and did not drop pebbles into the final nest closure (instead placing them into the closure). Ponder's 'population 2' consistently used a pebble tool to buzz-pack the nest closure. Whether these differences reflect intraspecific or interspecific variation in behavior is unclear.

Progressive provisioning appears to occur in isolated terminal taxa scattered across the phylogeny of the Sphecidae, suggesting that evolution away from this behavioral state has been rare (Field et al. 2020). The Field et al. (2020) phylogeny also currently reveals no example of a multi-species clade of exclusively progressive provisioners. Additional work is required to determine if the multiple species within the *A. pruinosa* species group represent such a clade of progressive provisioners. Members of the *A. pruinosa* species group may also provide opportunities to ask if evolution away from progressive provisioning has occurred. Additional taxonomic and behavioral work on this species group is needed to yield insights into these questions.

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