Research Article

Nesting Behavior of *Abispa ephippium* (Fabricius) (Hymenoptera: Vespidae: Eumeninae): Extended Parental Care in an Australian Mason Wasp

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The genus *Abispa* includes Australia's largest wasps, potters with distinctive mud nests weighing up to 0.5 kg. During 31 days near Katherine, NT, Australia, we observed 8 active *A. ephippium* (Fabricius) nests and dissected 16. Nesting is lengthy and asynchronous; female generations often overlap. Females display long-term parental care through truncated progressive provisioning, removing debris, repairing damage, and attacking potential invaders. Males patrol water-gathering spots, and visit and associate with active nests, mating there and in flight. Females actively guard nests, but challenged nest-attending males simply retreat. The distinctive funnel-shaped entrance helps females defend nests physically but probably not chemically; dismantled for cell closure material, it is built anew for each cell. Nests contain up to 8 cells; construction and provisioning total about 7 days per cell. The only parasite was *Stilbum cyanurum* Forster. Thievery and nest usurpation by *Pseudabispa paragioides* (Meade-Waldo) were discovered.

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1. Introduction

Restricted to Australia and New Guinea, the 6 described species of *Abispa* wasps are solitary-nesting mason or potter wasps that in the words of an early biologist, “take the palm for being one of the largest and handsomest” [1]. *Abispa* are in fact the largest Australian wasps, measuring up to 40 mm long, and their red/orange/yellow and black coloration is both striking and conspicuous. Their massive mud nests (Figure 1)—first described [2] in 1850—are equally outstanding, with a downward-pointing funnel-shaped entrance tube and unusually thick (up to 16 mm) mud walls. Nests commonly can weigh half a kilogram.

Knowledge of *Abispa* biology is sparse, limited to a few brief reports summarized elsewhere [3]. Although the wasps themselves are not uncommon in entomological collections, their nests are widely dispersed, well camouflaged, and often hidden in well-protected locations. The only long-term study [4] of nest construction behavior for any *Abispa* was based on observations of a single nest of *A. ephippium* (Fabricius);

it documented that females of this species were long lived (>2 months), and that nests were constructed slowly and were provisioned with caterpillars. There also has been only one report [5] of *Abispa* sexual behavior; it showed that males of *A. ephippium* and *A. splendida* (Guérin-Méneville) patrolled areas where females regularly collect water (an essential commodity in short supply in arid Australia) and perhaps at nests as well, and that males mated repeatedly at these sites with no evident courtship preliminaries.

Here, we report the first detailed behavioral study of *Abispa*. We provide new information on nest construction, provisioning, defense, usurpation, parasitism, and mating, with a unifying focus on the parental care displayed by females of *Abispa ephippium*.

2. Methods

2.1. Study Site. Nesting behavior was studied at the Northern Territory Rural College campus of Charles Darwin University, 15K N. of Katherine (S14° 22.545' E132° 09.403').

FIGURE 1: Typical nests of *Abispa ephippium* Perkins from Katherine, NT, Australia. (a) A newly constructed single cell nest lacking the smooth exterior mud layer that characterizes older nests. (b) A mature nest with 7 cells (funnel out of view on back side) with a visiting male lurking at the back. The wasps measure about 35 mm long.

Nests were located on and beneath various campus buildings, always in rain-sheltered, low-light niches. Long-term observations were conducted principally under the drive-through carport and laundry area of a “Queenslander” style residence and around a small temporary pool nearby formed by a leaking hose fitting in the yard (Figure 2); in 2004 we simultaneously monitored nests on a daily basis at several nearby buildings.

2.2. Study Dates. Field studies were conducted from 27 November to 10 December 2004 and from 17 November to 5 December 2007, calendar intervals that correspond to a period of increasingly frequent rains that herald the rainy season in northern Australia. Heavy rains occurred intermittently, especially in the evening and at night, during both years. Daytime high temperatures generally ranged 90–95°F (31–35°C).

2.3. Behavioral Study Methods. To enable individual recognition, nesting female *A. ephippium* were netted and marked on the thorax, abdomen, or both with unique combinations of spots of white, green, and silver Liquid Paper correction fluid. Other individuals of both sexes flying through the area or visiting the small pool were opportunistically captured and also marked.

During each nesting season, a focal nest was chosen for detailed behavioral observations. The focal nest for 2004 was observed for a total of 58 hours spread over 14 days, during which 2 cell construction cycles were observed. The focal nest for 2007 was observed for a total of 63 hours over 11 days. In 2004, 4 additional nests were monitored daily; in 2007, 2 additional nests were collected after shorter observation. Digital photographs and video clips were obtained for documentation and more detailed analysis. At the conclusion of the field studies, all nests were collected and dissected.

2.4. Challenge Presentations. To roughly simulate encounters with natural parasites at different stages of construction or

FIGURE 2: Study sites. (a) Drive-through carport of a residence on the Charles Darwin University Rural Campus 15 km North of Katherine, NT, Australia, that was the main study site in both years. *Abispa ephippium* and other mason wasps nested among the carport rafters. (b) Small temporary pool under a mango tree in the residence yard; it was regularly visited by both *Abispa* sexes in 2004.

provisioning, resident females associated with 3 nests were challenged with freshly killed bombyliid flies and chrysidid wasps either affixed to the end of a long flexible palm-frond straw (Figure 3) or glued directly onto the nest exterior (Figure 4) using Elmers school glue. In addition, at other

FIGURE 3: Intruder experiments. (a) A freshly killed cuckoo wasp (*Chrysis* sp.) and (b) a bombyliid fly (*Thraxan* sp.). When presented to a female *A. ephippium* at different stages in nest construction, both elicited a strong aggressive response.

FIGURE 4: Experiment with a *Thraxan* “intruder” glued to nest surface (a). When the female encountered the fly, she attacked it viciously (b). Nest funnel diameter 15–17 mm.

times, we similarly presented either an insect-sized three-colored bead model or a freshly killed (by freezing) individual of either the social vespid *Ropalidia* or the gregariously nesting sphecid *Sceliphron formosum* (Smith), 2 species that commonly nested at the study site but were never observed to interact with *Abispa*. Because we had so few active nests, we did not intend these to be replicated, systematic, well-controlled experiments, but instead, preliminary “concept” trials.

Because the function of the funnel-shaped nest entry of *Abispa* and some other mason wasps is largely unknown, we also undertook preliminary trials to test for evidence that the funnel surface might repel the foraging *Pheidole* ants that were common in the study area. We removed fresh funnel fragments (100–200 mm²) from active nests, placed them with the smoothly brushed inner side up, and baited each center with a small (8–12 mm) paralyzed caterpillar stolen from *Bidentodynerus bicolor* (Saussure) (Vespidae) that were nesting at the same site. Care was taken to handle funnel

fragments and caterpillar baits only with forceps. Paired controls were mud fragments of similar size gathered nearby from a naturally cracked dried puddle. Baited fragments and baited controls were arranged in random order along an active ant trail at intervals of about 10 cm and about 2–3 cm to either side of the trail (Figure 5). We exposed the baits simultaneously for 20 minutes and recorded the elapsed time until the caterpillar was discovered and then fully removed from its mud platter.

2.5. Voucher Specimens. Voucher material was compared with authoritatively identified specimens deposited in the CSIRO Insect Collection in Canberra, ACT, and specialists subsequently verified our identifications (see Acknowledgments). Specimens from this study are deposited in the CSIRO Insect Collection; the University of California, Davis (Bohart Museum); the American Museum of Natural History; and the University of Georgia (Fattig Entomology Museum).

FIGURE 5: Experiment to test possible repellency of *A. ephippium* nest funnel to ants (*Pheidole* sp). Funnel pieces were randomly paired with dried mud fragments along either side of a natural foraging trail. Each was baited with paralyzed caterpillars, and their removal by recruited ants was timed. Inset shows ants cooperating to remove a bait.

FIGURE 6: Daily number of *A. ephippium* males and females marked at the study site in 2004.

3. Results

3.1. Marked Wasps. During the 2004 field study, we marked 46 wasps (15 females; 27 males; 4 of undetermined gender) over the course of days (Figure 6). Initial capture was at either our principal study area (18 individuals), the small pool (13 individuals), or nearby buildings monitored periodically (15 individuals). Some of the “cruising” individuals marked, later recaptured, and kept as vouchers subsequently were identified as *A. meadewaldoensis* Perkins, which is morphologically difficult to distinguish from *A. ephippium* (J. M. Carpenter, unpublished), but all nest voucher females were

A. ephippium. Four marked females had active nests under observation, and thus were regularly observed. Another 15 wasps (6 females, 9 males) were seen or recaptured on subsequent days at least once during the study; of these, 6 (2 females, 4 males) were recaptured 2 or more times; one male was recaptured 5 times at 3 different locations.

In 2007, wasp numbers and nesting activity were poor by comparison with 2004. We again captured and marked all wasps seen, but only from the carport area because the pool was now dry. Although we checked other nearby buildings, we did not capture or mark any individuals from those structures. Of the 16 wasps marked at the principal study site, 10 were females and 6 were males. One marked female was regularly seen because she had an active nest. Another 5 wasps (2 females and 3 males) were seen or recaptured on subsequent days—1 male and 1 female reappeared once, 1 female was seen 3 times, and 2 males were seen or recaptured on at least 4 or more days.

3.2. Daily and Seasonal Cycle. Females were active at nests from just after sunrise until just before sunset. Windy or rainy periods appeared to have little effect on nesting progress. Nights were typically spent away from the nests. A photograph of a single sleeping *Abispa* from Brisbane, QLD, Australia, is posted on the Internet [6], the first such record for this genus; we found no sleeping *Abispa* at our study site.

Depending on nest phase or cell development, females often backed into the funnel and up into the cell to rest motionless with their head facing out, their antennae barely visible. Here they sometimes remained for extended periods (sometimes more than 1 hour). At irregular intervals, they would leave the nest for brief periods, and upon returning usually checked the current cell intensively, often making several inspection circuits around the nest exterior as well.

It appears likely that nesting occurs asynchronously within the *Abispa* population. At least 4 and probably more successive generations occur annually at the study site. We have eyewitness records of adult *A. ephippium* flying around the study site for various dates during every month between September 8 and May 24, which corresponds to all but the very driest “winter” months in northern Australia.

3.3. Nest Location. Unlike sphecids mason wasps such as *Trypoxylon* or *Pison* that often cluster their nests in suitable places, *Abispa* nests are isolated. In 2004, in an intensive search of an approximately 5-acre area that housed 10 faculty residences with covered outdoor areas that appeared suitable for *Abispa* nests, we located 5 active nests and 7 old nests. In 2007, extensive searching of this same area plus an adjoining area of 15 additional buildings (dormitories, classrooms, and administrative offices) revealed only 2 active nests and 3 old nests. (Some residents reported knocking down nests, however). The only nest found that was not associated with human-built structures was an old nest in a protected tree crevice about 1 m above the ground near the principal study site, but we did not search extensively.

The height above the ground varied. Some nests were within 5 cm of the carport floor; others were among ceiling joists. All nests were attached to 2 adjacent surfaces, such as the junction of an exposed ceiling joist and the ceiling. None was affixed only to a single flat surface. Nests tended to be quite securely attached, tightly conforming to the dimensions of the space. Some occurred in quite unexpected places, for example, in an enclosed space under the seat of a child's plastic motorcycle.

3.4. Nest Construction. A typical *Abispa* nest is built in stages. A cylindrical cell is begun in a relatively dark and hidden corner; the only clue that it is not an inorganic mud blob is the decidedly conspicuous flared funnel that soon extends from its open end (see Figure 1). Average interior dimensions of a cell before funnel construction are 28.7 mm long by 11.8 mm diameter (length range, 23–36 mm; diameter range 9–17 mm; $n = 51$).

Females constructing cells work steadily with little interruption. It took our focal female 4.75 hours and 74 mud-gathering trips to build a single cell to the point of beginning the funnel. Two h and 19 mud trips later, the funnel was constructed. Another 38 minutes were spent at the nest, fine tuning it. The funnel is surprisingly delicate for such a large structure, being less than 1 mm thick at the rim. From an internal diameter of just over an *Abispa* head width (about 9 mm), where it connects to the cell, the bell opening flares to 14–17 mm diameter at its open end; the total length of the funnel is about 20 mm, depending on the point to which one measures.

Inside the empty cell, the female lays an egg. For the next day or 2, she mostly stays within the nest, with her head facing the entrance. Occasionally, she will come out and wander about the nest exterior as though inspecting it. At a time presumed to correspond to egg hatching (in one case, 27.5 hours after apparent oviposition), she leaves and returns with a caterpillar that is placed inside the cell. This may be repeated once or twice. Then she resumes her watchful waiting. Over the next 2–4 days, at decreasing intervals she will bring a few more caterpillars, almost always of the same species and size range. On the final day of provisioning (about 6 days after cell construction), she repeatedly returns with caterpillars, then abruptly stops. This pattern of provisioning is termed truncated progressive provisioning and appears to be characteristic of *Abispa* species [3].

Between provisioning trips, internal nest care is practiced. Periodically and especially toward the end of a cell cycle, *Abispa* undertook episodes of apparent cell cleaning. Repeatedly, she would enter the cell head first, then back part way out through the funnel, sweeping with her foretarsi, and in the process jettisoning bits of debris.

Mud for the final cell closure is obtained by dismantling the funnel, one mouthful at a time. *Abispa* can soften and remove a half-dozen pellets of mud with a single load of water ($x = 6$ pellets, range 5–8); she requires about 30 seconds to remove a pellet and another 30 seconds to reapply it to the cell closure or nest wall. Thus, while dismantling

FIGURE 7: Schematic plan of a typical mature *A. ephippium* nest architecture, showing cell arrangement and construction order.

can take almost as long as initial funnel construction, it is time spent almost entirely on the nest rather than away. In timed observations, our focal female in 2004 took 1.5 hours to completely eliminate her funnel, but after the first 45 m the cell was completely closed by funnel mud. She was away from the nest only 19 minutes—4 trips before the cell was closed and other 2 after that for additional water used to obliterate all traces of the funnel. By comparison, collecting the funnel mud involved being away from the nest for 81 m.

At intervals of about a week, construction begins on a new cell as the cycle is repeated again and again. Although some nests are abandoned due to factors such as untimely female death, a complete nest typically has 6–8 cells ($x = 5.6$, $SD = 1.9$, $n = 15$). New cells are added below, or less typically above, existing cells in a fairly stereotyped order (Figure 7). No nests were more than 2 cells thick, and the greatest number of cells found in any nest was 8. The largest nest exterior dimensions were 80 mm $\times$ 54 mm $\times$ 38 mm.

When first built, the exterior of a new cell is bumpy, coarse, and quite conspicuous, even after funnel deconstruction. However, at intervals that can span several days, the female alternately inspects the nest exterior and brings numerous mud pellets that she plasters over it, gradually filling in the valleys between cells, thickening the cell wall, and further securing nest edges to the substrate. During these plastering bouts, the female works steadily; after applying each mud pellet, she departs immediately, usually without grooming or further nest inspection. Between bouts, she generally resides within the nest, facing outward; it was during such intervals that we opportunistically conducted nest defense experiments (described hereafter).

Toward the end of the wall-plastering phase, the nest exterior increasingly takes a smooth, shiny appearance as the female works intensively, mouthing a circumscribed area repeatedly. It is generally difficult to detect any liquid being added, but sometimes there is a serpentine wetting that is briefly visible before it dries (Figure 8, arrow). The result is a smooth rounded fortress with walls of variable thickness

FIGURE 8: Female *A. ephippium* applying liquid to nest surface; arrow shows the serpentine drizzle applied most recently by this female.

(range 6–10 mm; $n = 25$ measurements on 8 nests). When nests are broken open, one can usually discern 2 distinct layers; the inner layer represents the initial cell construction, and the outer layer is the added mud plaster (see [3, Figure 3]).

3.5. Mud and Water Foraging. We have used the term “mud foraging” to describe trips that culminated with a female returning with mud in her mandibles. However, like other eumenid mud wasps, *Abispa* does not collect mud directly but fills her crop with water at one site and makes mud from soil at another location called a quarry [7]. Mud-foraging trips in 2004 averaged 230.4 seconds (range 45–1191, SD = 108.0, $n = 158$). The task of applying the mud load to the nest surface averaged 158.7 seconds (range 21–494, SD = 69.2, $n = 165$).

Once a suitable water source is identified, females appear to return repeatedly to it. One marked female was observed returning repeatedly to drink for 10–30 seconds from the small pool; over a 2-hour period, she made 12 successive trips, returning about every 9 minutes ($x = 540.1$ seconds, range 188–831). On her ninth visit, a male simultaneously arrived and pounced on her immediately; they then flew off *in copulo*. She returned to her drinking spot 707 seconds later.

3.6. Funnel Construction and Maintenance. Funnel construction is a major undertaking. Whereas it took our 2004 focal female 4.75 hours to make a basic cell, it took her another 2 hours (and 19 trips) to construct the basic funnel and an additional 38 minutes to brush it smooth. Forming a large funnel from mud is a significantly more precise task than building a cell; applying each load of mud to build a cell took an average of 131.2 seconds (less than spent on plastering surface mud), but applying mud to the funnel averaged 186.4 seconds ($P = .005$, t test).

During funnel building, a female works steadily, except for the distraction from mating attempts by one or more males that may be present during much of this phase

FIGURE 9: Foretarsus of *A. ephippium* showing ventral tufts of setae on each tarsomere used to polish the interior surface of the entrance funnel.

(described hereafter). To make the funnel, a female wasp stands on the nest, gripping it with her mid and hind legs. While her head is inside the incipient funnel bell, her forelegs manipulate the pellet of mud from her jaws. She applies the pellet to the funnel rim, slowly rotating her body in such a way that the rim edge is kept even. At variable intervals she pauses, grips the funnel rim with her middle and hind legs, and synchronously applies her mouthparts extensively to the inner surface of the funnel with a vigorous bouncing movement, a ritual we termed “mouthing.”

The smooth, almost polished interior surface of the funnel bell is regularly maintained by brushing with dense tarsal setae unique to *Abispa* females (Figure 9). The brushing ritual encompasses several bouts during which the wasp crawls headfirst into the funnel, then slowly walks backward out to the funnel rim while scraping her foretarsi in unison rapidly and repeatedly over the funnel’s inner surface. As she starts each bout in a brushing sequence, she shifts her body slightly around the rim, so that the sequence tracks either clockwise or counterclockwise and sometimes ultimately covers a full 360°.

Complete coverage of the funnel required an average sequence of 9 brushing bouts (range, 7–16, $n = 9$). Funnel maintenance via brushing sequences continues at irregular intervals while oviposition, provisioning, and nest plastering are taking place. There seemed to be no particular external stimulus that initiated brushing bouts, but in the hour following one of our experiments with intruders (described hereafter) brushing frequency noticeably increased. In that instance, the female performed 9 separate extensive brushing sequences in succession, more than what had been seen at any other time. This female also did frequent nest exterior inspections and groomed extensively following the experiments.

To assess *Abispa*’s repair propensities, we purposely removed entrance funnels from 3 active nests. All were at least partially repaired immediately thereafter though the replacement funnels were smaller and less symmetrical than the originals (Figure 10). On another occasion when one side of a nest that originally had been loosely attached to a board was purposely exposed, the resident female switched almost immediately from cell construction and spent most of 2 days plastering mud to cover, smooth, and secure the exposed face (Figure 11). Inspired by this observation, we used an

FIGURE 10: Funnel repair by *A. ephippium*: (a) Intact funnel, (b) funnel artificially removed, (c) first mud load applied by female, and (d) completely rebuilt funnel with female in characteristic head-out resting position. Entrance hole diameter 9 mm.

FIGURE 11: Nest before (a) and one day after (b) the front surface of the nest was exposed by removing the board against which it had been built. Note newly added mud over the exposed surface. Nest length 75 mm.

emory board to file a small area on the exterior surface of an active nest to see whether the female would respond to a lesser abrasion; she did not react to the abraded area, but this observation is inconclusive because her exposure to it was relatively brief since for unrelated reasons this turned out to be the last afternoon of her tenure on the nest.

3.7. Prey. Prey foraging involved a considerable investment of time and energy. Thirteen timed trips in which the female returned with a prey caterpillar averaged almost 20 minutes each ($x = 1179.7$ seconds, range 433–2680, SD = 662.4). Once she arrived back at the nest with prey, the wasp typically spent just under 3 minutes at the nest before leaving again ($x = 179$ seconds, range 32–466, SD = 141.5, $n = 11$).

Paralysis of prey is light, and the caterpillars continue to defecate. Prior to pupation, the wasp larva produces a tough parchment-like cell lining that walls off prey fecal pellets and other debris at the distal end of the cell (Figure 12). Two old *Abispa* nests contained cells where the wasp larva had died or failed to develop; 2 prey had pupated in each, and one ultimately eclosed in each, allowing identification of the adults as Pyralidae, probably Phycitinae, and Crambidae, probably Pyraustinae.

Larval prey identifications are difficult because Australian caterpillars are relatively poorly studied. We collected the contents from 2 cells in 2004 and one in 2007 (Figure 13). One cell from a 2004 nest held a large wasp larva and 13 caterpillars of apparently a single species; the other held a large wasp larva and 5 caterpillars that appeared to belong to 2 species. From the 2007 nest cell, we recovered 9 caterpillars of apparently a single species; because this nest was found on the carport floor after falling from the rafters during the night, it originally may have included additional prey.

Food thievery is well known and relatively common among various solitary wasps [8]. We documented prey theft

FIGURE 12: Fragment of opened *A. ephippium* nest showing parchment-like cell lining made by the mature larva. The walled off area shown at the upper end of the cell contained waste materials, cell length 28 mm.

by *Pseudabispa paragioides* (Meade-Waldo) from an active *A. ephippium* nest in 2007. The female came to the nest while the *A. ephippium* female was away and immediately entered the open cell, exiting quickly a few seconds later carrying a caterpillar.

3.8. Mating. Courtship preliminaries are absent but multiple brief copulations are clearly common ($\bar{x}$ = 61 s, range 42–86, n = 9), both at the nest and at water sources. In 2004, males were regularly recorded to visit 3 active nests and several copulations were observed there (Figure 14). The most detailed documentation occurred on the afternoon of May 12, 2004. During the six-hour period in which a female was constructing a new cell and beginning to make a funnel, a single male (green-spot) was continually present and was observed attempting to mount her unsuccessfully at least 7 times. The next morning the funnel was complete by about 0930, but the green-spot male was gone and a new male (2 white spots) was present. The latter was seen to copulate with her successfully 3 times in succession (for 69, 86, and 52 seconds, resp.) between 0940 and 1000, after which he departed. Less than 10 minutes later, the green-spot male arrived, immediately mounted the female, and successfully copulated for 67 seconds. Thus, this female mated at least 4 times with 2 males; probably all were prior to ovipositing in her newly completed cell. Interestingly, 2 days earlier a different marked male had been recorded on this same nest, but no interactions with the female had been observed.

In 2007, the female of our focal nest was observed to copulate 7 times with 3 marked males that visited her nest. One marked male (Figure 14) was observed to mate with her 5 of those times over 2 days as she was completing a new cell and funnel; this same male was seen to approach the nest at least once and usually several times a day over a period of 10 days, including 5 days after the original female had been usurped by *P. paragioides* (described hereafter).

Mating also occurs away from the nest. In 2004, 2 copulations were recorded that were not nest-associated. At 1840 on July 12, 2004, the marked female from our focal nest was netted *in copulo* with an unmarked male as they flew along the rear of the carport. The other occurred the next day at 1545, when a male at the temporary pool mounted a drinking female and the pair flew off *in copulo*.

Nesting females often appeared to simply tolerate mating as a brief interruption of other activities. The one female observed to mate 3 times in succession on her nest with the same marked male and once with a different male simply resumed whatever task she had been doing, seemingly unfazed by the interruption. However, a day earlier this same female repeatedly rebuffed one of the same males' attempts to copulate. Thus females appear to be able to exercise some choice and may not be entirely passive to male mating attempts; receptivity may be modulated by nest stage or ovarian development.

Even though nests are isolated, solitary, and in unpredictable locations, and the nest stage changes cyclically, females at active nests clearly are valuable resources for males. How males locate active nests or whether nest or female odor is involved is unresolved, but males probably learned the location of active nests for they were frequently observed to fly directly to them, approaching and landing with no hesitation. At least some males associate with particular nests for extended periods. In one case, a male was continuously present on a nest throughout much of one day while the female was bringing and applying mud plaster; although the male repeatedly attempted to mount the female, she showed no interest and was not interrupted in applying the mud. This male made at least 6 unsuccessful attempts to couple. Two other marked males remained associated with another nest for extended periods on 2 successive days, again during a period when the female was regularly bringing mud; however, in this case each was seen to successfully mate at least once with the female. If a male was present when a female was "resting" in her funnel (discussed earlier), he often remained for long periods on the exterior of the nest not far from the funnel entrance; however, males were never seen to enter the nest funnel.

On many occasions, individuals flew quickly through the study site without pausing. We counted 149 of these flights during the 10 days of our 2004 study. Most (73.8%) occurred during the morning hours (Figure 15), and the activity peaked in early December. To describe such behavior, a reviewer suggested the term "patrolling," a term generally defined as regular tours of movement to guard or protect a place or maintain order. However, we saw little evidence of such a purpose for these particular flights. Thus, we prefer to provisionally call this behavior "cruising," a recognized slang word for frequenting a public place in search of a sexual partner. Flying speed and the general similarity of the sexes precluded identification of the sex of flying individuals on the wing, but based on captures, most were males. We assumed that they were seeking females, because in a few cases we observed pairs flying *in copulo*. Obviously, resolving the purpose of such flights (and thus the proper terminology to use) will require further study.

FIGURE 13: Prey from 3 nests of *A. ephippium*. Caterpillars in the left and center frames were removed from nests collected in 2004; those shown in the right frame were from a 2007 nest.

FIGURE 14: Mating in *A. ephippium*. (a) Marked male attending a nest where the female is resting in her nest entrance. (b) Copulation on the nest; note the female's exerted sting. (c) Another pair mating on their nest. (d, courtesy of Bonnie Heim) Male has landed on a female obtaining water at the small pool.

This is not to discount the possibility of territorial behaviors, however. In 2007, the marked male most associated with our focal nest was also repeatedly seen perched at one lower corner of a window air conditioner unit about 15 m from the carport, to which he returned after brief chases of other wasps or periodic flights back and forth along the length of the house. Females visited the AC unit regularly,

entering through the grill, presumably to obtain water from the corner of the condensation pan. This male attempted to mate with these females, and was observed to chase and pursue other wasps, probably males. He remained in tenure at the same spot over several successive days. The patrolling behavior occurred intermittently throughout the day, but was more intense in the last hour before sunset; whether

FIGURE 15: Daily number of *A. ephippium* wasps recorded as patrollers or “cruisers” that flew through the study site during the morning hours as compared to afternoons in 2004.

this behavior constitutes true territoriality and therefore an additional *Abispa* male mating strategy also will require additional study.

In 2004, males regularly visited a small temporary pool (see Figure 1) that was frequented by other males of both *A. ephippium* and *A. meadewaldoensis* and by females coming to obtain water. During one 2-hour period, a marked male was recorded to visit the pool 10 separate times. On another occasion we placed 2 freshly killed (by freezing) males in realistic resting positions on decaying mango fruits at the water’s edge and watched patrolling males’ responses for 3 hours (0900–1200). Although male *Abispa* visited the pool 22 times during this interval, they displayed no obvious interest in the dead males.

3.9. Reuse of Old Nests. Nests often persist for a long time after the original *Abispa* occupants emerge. There is no evidence that *A. ephippium* reuses its old nests or cells of other species’ nests. However, cavities left from emerging wasps are highly attractive to various secondary “renters”—bees and wasps that remodel and adapt them for their own use. Six species of secondary nest users were regularly observed at our site: a megachilid bee (*Chalicodoma aethiops* (Smith)), a sphecid wasp (*Pison* sp.), and 4 smaller eumenids (*Paralastor* sp., *Bidentodynerus bicolor*, and *Epidodynerus tamarinus* (Saussure) and *E. nigrocinctus* (Saussure)). Each of these was documented to reuse emerged cells of old *Abispa* nests as well as old *Sceliphron* nests. Biological notes on some of these are to be published elsewhere.

3.10. Development. The 6 mm long egg is suspended from a short (0.5 mm) thread near the distal end of the empty cell (see [3, Figure 4]). Extrapolating from data on emergence times, number of nest cells, and our records for the time to complete a single cell, it appears that (except for the driest

“winter” months of June through August) development from egg to adult requires 4–6 weeks.

Overlapping generations are common in *A. ephippium*. Fairly often, the first progeny complete their development while newer cells of the nest are still under construction. At the 2007 focal nest, at least 2 cells emerged while the nest was still active. In 2004, three nests that were collected while females were still in attendance were found to contain mature pupae or teneral adults. Female eggs are probably laid first; in the 4 cases where we obtained mature offspring, the earliest (oldest) nest cell yielded a female.

3.11. Cleptoparasitism. While the marked resident female at our 2004 focal nest was away from her nest, an unmarked *A. ephippium* female discovered the nest, entered, backed out, reentered, backed out, and then flew off. About 2 minutes later she returned and flew directly to the nest, again entering it. The tip of her abdomen was visible over the next several minutes of activity inside the nest. Repeatedly ($n = 6$) she backed partway out, then crawled back in headfirst so that she was entirely inside the cell. Then she backed all the way out, turned around, and backed into the nest so that her head and antennae were all that were visible in the funnel entrance. This newcomer then took up residence, resting partway into the cell with her head facing out inside the funnel, for nearly 4 hours before departing. Curiously, the focal female was away from the nest this entire time—the only time we observed such an extended leave of absence from a nest during active provisioning—and she did not return for the first time until 29 minutes after this unmarked female departed. At first upon her return, her behavior did not appear unusual. However, after briefly resting motionless in the funnel with her head facing out, she moved out onto the nest surface and began 45 minutes of intense activity—making several very thorough inspection circuits, thoroughly brushing the inside surface of the funnel, and occasionally mouthing the funnel’s exterior—punctuated with bouts of grooming. Finally, although it was late in the day (1715), she brought in at least 4 caterpillars after this time.

3.12. Nest Usurpation. Several lines of evidence and direct observation, to be published elsewhere, show that female *Pseudabispa paragioides* regularly usurp or supersede *A. ephippium*. These usurpers were common at the study site, especially in 2007 when we captured and marked essentially equal numbers of *A. ephippium* and *P. paragioides* (16 versus 15, resp.).

In 2004, we discovered an active usurped nest with a *P. paragioides* female already present (Figure 16), and recorded 2 *Abispa* nests that contained a cell from which a male *P. paragioides* emerged. There was no way to determine whether the *Abispa* female collected in the 2004 nest that yielded an adult male *P. paragioides* was the original nest-founding female. However, in 2007 we obtained positive proof of the usurpation propensity of *P. paragioides* females and were able to document this usurpation behavior, including vicious and ultimately fatal fighting (Figure 17).

FIGURE 16: (a) A single-celled nest of *A. ephippium* that was occupied by a *Pseudabispa paragioides* female when discovered. (b) This same nest was found to contain 20 caterpillars and an egg (arrow), having been mass-provisioned by the *P. paragioides* female.

FIGURE 17: A marked female of *Pseudabispa paragioides* (upper individual) in a battle with a female of *A. ephippium*; shortly after this photograph was taken, the stung *Abispa* female died from the venom of *Pseudabispa* and the latter took over her nest.

3.13. Parasites and Other Nest Enemies. Several relatively ubiquitous parasitoids of other mason wasps such as miltogrammine flies (*Sarcophagidae*) and *Melittobia* wasps (*Eulophidae*) commonly gain access to mason wasp nests via the open nest entrance during provisioning. These parasitoids were common at the study site and were reared from nests of other mason wasp species. However, *Abispa* nests at our study site showed a remarkably low level of parasitism. In 2004 none of the 5 active *A. ephippium* nests collected were parasitized, and the only parasitism in 2007 was the chrysidid attack outlined in what follows.

The relatively large chrysidid *Stilbum cyanurum* Forster was common at the study site. In 2007 we observed this chrysidid to land and briefly investigate our focal nest while the female was away. Eight days later at the same nest, the usurper *P. paragioides* (see above) likewise was temporarily

away, having been actively on the nest provisioning a cell 24 minutes earlier. Suddenly a chrysidid appeared and landed on the nest with no hesitation, suggesting previous knowledge of the nest. During subsequent days we recorded what appeared to be the same chrysidid visiting this nest at least once daily, but unfortunately were unable to mark the individual. During one such visit the chrysidid flew back and forth a few cm in front of the nest for nearly 1 minute as though memorizing landmarks, then landed and briefly crawled upon the nest and adjacent substrate for about 12 seconds before flying away. On another occasion, the chrysidid approached as the resident *P. paragioides* was actively mouthing an area on the lower part of her nest; it did not attempt to land but flew off after only 10 seconds with no evident notice from the resident female.

At the time of its attack, *S. cyanurum* first walked about briefly on the lower (older) nest surface, but quickly focused on a small area and began to chew into the mud at a location that upon nest dissection proved to be cell 1 with a late stage *Abispa* pupa (Figure 18, left). After just over 1 minute of chewing, the parasite reversed position and thrust her ovipositor into the newly made hole (Figure 18, right). Oviposition was completed within 15 seconds, after which she again reversed position and began to refill the hole with mud chips. The entire process lasted about 9 minutes. When the *Pseudabispa* female arrived 10 seconds later, she did not initially detect the chrysidid, which had retreated to the bottom of the nest, but within 30 seconds she began to patrol the nest surface and upon encountering the chrysidid, immediately chased it away. As soon as she departed on another provisioning trip, however, the chrysidid returned and spent another 9 minutes filling the rest of its oviposition hole before finally departing. Later nest dissection revealed that in addition to the parasitism of cell 1 that we observed, a second cell immediately above it had also been parasitized and contained a similar-sized chrysidid larva feeding on the host prepupa.

Lizards and spiders are likely to be common enemies of mud wasps; dead wasp mummies were regularly seen in old spider webs at the study site. Large huntsman spiders (*Holconia* sp.) also frequented the rafters and individuals were seen near nests, but no predation by or upon these arachnids was observed. An Asian house gecko (*Hemidactylus frenatus* Schlegel) rested adjacent to one active *Abispa* nest for 3 consecutive days. It seemed not to notice the comings and goings of the relatively large wasp; likewise, the resident wasp paid no obvious attention to it.

3.14. Challenge Presentations. Do *Abispa* actively defend their nests, and if so, how? Because parasitic bombyliid flies were commonly seen at our study site and are known to parasitize many solitary wasps and bees [7], we glued freshly killed bombyliid flies (*Thraxan* sp.) to flexible palm frond fiber straws (see Figure 3, b) and presented one to a female resting inside her nest funnel, head facing out, at the midpoint of a cell construction cycle. She quickly lunged out, decapitated the fly in an instant, then retreated into the nest. A second fly presented minutes later also elicited a similarly

FIGURE 18: *Stilbum cyanurum* attacking a nest of *A. ephippium*. The parasite chews a hole through the nest wall (a), inserts her telescoping abdomen into the hole to oviposit (b), and refills the hole with mud. Inset shows the chrysidid larva consuming an *Abispa ephippium* pupa found in the cell upon later dissection.

rapid response; she grappled with this fly and removed its right wing. After the second encounter, the female briefly flew off the nest but returned to take up her resting position in the cell entrance after 143 seconds. Over the next hour she performed 9 separate bouts of funnel brushing. Then we exposed her to 3 more similarly presented flies sequentially over about 10 minutes. Each fly was viciously attacked, bitten and partially dismembered, after which the female retreated to rest in her nest entrance, head facing outward, never once flying from the nest.

Three days later, we repeated these experiments at 2 other nests and again at the focal nest when the female was constructing a new cell. At the first of these nests, the female was resting inside. When challenged by a more or less stationary fly as before, she responded immediately by lunging repeatedly with opened mandibles, flying off briefly, and then returning to inspect the nest exterior. We challenged her a second time, wiggling the straw such that the fly appeared to hover immediately in front of her. At this, she responded with a brief wing buzz but no lunge or bite. As we continued the challenge, she did too, buzzing briefly 4 to 5 times in rapid succession. After 52 seconds with no physical contact, we removed the fly. After 12 minutes, we wiggled the fly at her once again. She immediately lunged, then wing-buzzed 3 times, twice, then 3 more times. Five more times we presented a jiggling fly, each time eliciting whirring wing buzzes until, after 57 seconds, she flew.

At the second nest, the female was away but a male visitor was resting on the exterior. When challenged with the wiggling fly on a straw, the male immediately backed away to hide behind the funnel, then came to the front side of the nest and took flight. There was no evidence of any nest defense, and the male was gone for 25 minutes before returning.

The final set of presentations with a fly on a straw was performed back at the original focal nest, where the female

was now in the early stages of constructing another cell. Her response was swift and “lethal” to 2 bombyliids offered in succession, and included biting off parts of their wings.

How would *Abispa* behave if a potential intruder were already present? Two days later, while the female was away we glued another freshly killed *Thraxan* sp. fly directly onto a nest below the funnel (see Figure 4). Returning with prey, the female apparently saw it, but with full jaws she crawled over the fly 3 times on her way into the funnel to place her prey in the cell. She then departed and returned with nothing after 8 minutes. This time upon coming to the fly she bit at it repeatedly; however, she was unsuccessful in dislodging it. After walking around the nest exterior as though inspecting for other intruders, brushing the funnel interior, and grooming a bit, she backed into the funnel. Over the next 65 minutes, the female left the funnel and approached the fly 7 more times, each time lunging repeatedly (8–19X, $n = 3$) without dislodging it, then groomed, brushed, and inspected in no particular sequence, and returned back into the funnel for increasingly long periods between bouts. An hour after these interactions, we removed the fly from the nest; it was “shopworn” but still intact.

We duplicated this procedure the same day at another nest with essentially similar results. In this case, the female was resting deep within the nest when we glued the fly on, and she immediately noticed it as she came out. She repeatedly alternated inspection circuits, short flights off the nest, circling the parasite, and lunging at it. She did not enter her funnel again until 12 minutes after initial contact, but then backed in, came out and lunged, and then backed in again to block the entrance. At this point, we removed the fly.

Given the violence of these attacks against dummy flies approaching or on the nest, it is probably unsurprising to note that later nest dissections showed no evidence of successful parasitism by bombyliid flies, despite their abundance at the study site and the fact that they were regularly observed flying along the rafters. These parasitic flies oviposit near solitary wasp nests, not directly within them. The *Abispa* female’s frequent cell cleaning episodes probably prevented this parasite’s larvae from successfully invading the cell.

Responses to freshly killed cuckoo wasps presented to wasps at the same 2 nests and in the same fashion as bombyliids also elicited strong responses (see Figure 3, (a)). For example, the first and second times that she was confronted by a cuckoo wasp inserted part way into the funnel, the female lunged at the intruder several times with such force that it could be felt through the straw. She bit at the intruder vigorously at each lunge, but it remained undamaged. Following a third confrontation, *Abispa* retreated deeply within her funnel, her head blocking the cell entrance; despite being actively nudged several times with the tethered parasite, she did not budge.

What factors release such aggressive behavior? We glued a small freshly killed *Ropalidia* worker to a straw and similarly presented it to our focal female just as she was finishing plastering some mud to the nest exterior. In 5 trials, each

FIGURE 19: Number of caterpillar baits removed from pieces of *A. ephippium* funnel mud and control mud pieces over a 20-minute interval.

lasting approximately 1 minute, she repeatedly lunged at the intruder but did not make actual physical contact. Then we presented a freshly killed *Sceliphron formosum* and (as a rough indication of visual rather than chemical cues) a “wasp” model of the same size constructed of 3 small colored beads threaded on a paperclip, each presented 4 times in succession for 1 minute, with about 2 minutes between trials. The female’s responses did not differ discernibly between the two actual wasp bodies and the bead-wasp; however, during the fourth trial with the bead model, she only lunged once. As with our other experimental manipulations, these were admittedly crude trials, done *ad hoc* under field conditions, but they seem to suggest that for *Abispa* visual cues such as a potential intruder’s size and apparent motion are more important than odor cues in threat recognition.

3.15. Does the Nest Funnel Deter Ants? Although others [9] have postulated that the funnel’s purpose is to protect nest contents against ants, paralyzed caterpillar baits were actually removed faster from the funnel pieces ($x = 325.4$ seconds, $SD = 217.6$) than from the field mud pieces ($x = 455.5$ seconds, $SD = 404.3$) and overall slightly more were removed from funnel pieces (21 versus 19), suggesting that wasp-made mud might even be attractive to foraging ants but certainly contained no repellents. However, as graphed data clearly illustrate (Figure 19), these differences were not statistically significant ($P = .2225$, t -test). Whether the frequently-brushed interior of the funnel acts as a physical “ant slide” would be an interesting topic for further study.

4. Discussion

Most aspects of *Abispa ephippium* nest structure and basic biology agree with those reported elsewhere for *A. ephippium* [4] and *A. australiana* [3]. Thick-walled nests are highly dispersed and lifetime female fecundity appears to be low (<10) with a correspondingly low immature mortality rate. Nest construction is slow, requiring approximately a week for each cell; coupled with the observed cell cleaning episodes and responses to potential parasites, this provides evidence for extended parental care.

Based on mark/recapture data, the overall sex ratio in the study population appeared to be male-biased. However, this may be an artifact, in that females tend to be nest-oriented and we located relatively few active nests whereas male mating strategies (described hereafter) predispose them to be more frequently encountered. Also, we discovered after the study concluded that some patrolling males were *A. meadewaldoensis*.

An *Abispa* nest with a stock of paralyzed prey is a valuable resource for a potential usurper, predator, or parasite. For a usurper, these equate to time and energy savings and reduced vulnerability to dangers associated with foraging. Like other solitary wasps, *A. ephippium* females are vulnerable to usurpation and parasitism because by necessity they must spend considerable periods of time away, leaving their nest undefended.

We documented that *P. paragioides* females not only usurp nests but also steal prey from partially provisioned cells of unsuspecting *A. ephippium* females while the latter are away from their nests. It is clear that *Pseudabispa* females regularly use existing *Abispa* nests and may obligatively do so. No unequivocal *Pseudabispa* nests were ever found despite extensive searching in 2 seasons.

It is generally believed [7] that cleptoparasitism has not evolved among solitary vespids as it has among sphecids wasps and bees, yet we observed behavior suggesting the possibility that an *Abispa* intruder entered a nest, destroyed the owner’s egg or newly hatched larva, then laid her own egg. This may be the first report of this behavior among the solitary Vespidae. Unfortunately, our evidence is circumstantial since we did not remove this nest until another week had passed.

Parasitism incidence was extremely low compared to levels experienced by many other solitary nesting wasps [10]. The only confirmed parasitism was the 2 cells in the focal 2007 nest that contained larvae of the cuckoo wasp *Stilbum cyanurum*. *Stilbum* species are reported to attack nearly every species of mud-nesting wasp in the Old World [11]. To date this is the only parasite recorded for *A. ephippium*. However, the bombyliid fly, *Thraxan* sp., used for challenge, was common at our study site, and although we did not confirm it to be parasitic on *A. ephippium*, it has been reared from nests of a related species, *A. splendida* [12].

The extraordinary thick wall that characterizes *Abispa* nests is a formidable barrier representing a considerable investment of parental effort. Its importance as a parasite deterrent was first suggested upon finding a very low incidence of parasitized cells in nests of a related species, *A. australiana*. Of 21 cells in 7 nests in that study [3], only 2

were parasitized, also by a chrysidid. In the present study parasitism occurred after the demise of the nesting female during nest takeover by *Pseudabispa*.

The extended parental care—including inspection, patrolling, active nest defense, and cell cleaning—practiced by female *A. ephippium* during the progressive provisioning of each successive cell appears to have restricted the nest's vulnerability to parasitism to the point in the nesting cycle where parental activity is waning or absent. Experimental results with other solitary nest-building wasps [13] also indicate that an extended period of parental attendance at the nest renders offspring less vulnerable to parasite attacks.

Our challenge presentations are the first indication of parental nest defense in *Abispa*. Females' vigorously aggressive attacks upon freshly killed cuckoo wasps, *Sceliphron*, *Ropalidia*, and even inanimate bead models demonstrated the active role females play in protecting their nests.

Because of the ubiquity and well-known polyphagy of *Melittobia* (Hymenoptera: Eulophidae) [14], we expected to find these tiny wasps parasitizing *Abispa*. However, although we confirmed the presence of *M. australica* Girault at our study site as a frequent parasite of other wasp and bee species and we confirmed that prepupae of *A. ephippium* were suitable and acceptable hosts (unpublished observations), *M. australica* was never found to have successfully parasitized this *Abispa* species. Likewise, unidentified satellite flies (Diptera: Sarcophagidae) were commonly seen at the study site. We never saw them pursue *A. ephippium*, and only once did we observe them following a *P. paragioides* female that usurped a cell in an *Abispa* nest; we later recovered 2 small maggots from among the prey in that cell. We suggest that the repeated cell inspections and cell cleaning practiced by *A. ephippium* females, in concert with truncated progressive provisioning, serve to minimize parasitism by these two common enemies of other solitary mud dauber wasps.

Construction of solitary isolated nests rather than clustered nests in groups is a third factor that probably contributes to the minimal parasitism experienced by *A. ephippium*. Evidence from other solitary wasps [7, 10] indicates that nest clumping may increase parasitism rates as well as prey theft by conspecifics.

Male mating behavior in *A. ephippium* has been studied previously for a population in New South Wales [5]. In the present study, multiple recaptures reconfirmed that *Abispa* males are highly mobile, appearing at different sites over several days. In the New South Wales study, male *A. ephippium* patrolled pools along an intermittently flowing stream and mated with females that arrived to obtain water. Our *A. ephippium* males also did not defend their water source, even though our pool was much smaller than the pools in the former study.

Based on recaptures and observations of marked individuals, it was clear that *A. ephippium* males practice more than one tactic in their efforts to locate receptive females. First, they regularly cruised through the study site where females were actively nesting. Second, they periodically visited and patrolled the small nearby pool where many females came to obtain water. Third, certain males were observed to visit and associate with particular active nests on a regular basis (see

Figure 14). Finally, possible defense of a point water resource (air conditioning unit) was also observed. It appeared that all of these tactics were conditional strategies practiced by individual males at different times, depending on local conditions. All strategies also appeared to be successful.

Copulations were most often seen at focal nests where we spent the bulk of our observation time, and copulation also was recorded at the small pool and a coupled pair was seen in flight at the study site. Mating on nests is recorded for both *A. ephippium* [4] and *A. splendida* [5]. With multiple copulations observed between marked individuals, our study has also confirmed the multiple mating previously described for *A. ephippium* [5]. Copulation duration ($x = 61$ seconds) and the absence of courtship preliminaries were also comparable to previous reports for *A. ephippium* [5].

Because hunting trips entail females being absent from the nest, often for extended periods, male presence on nests could potentially deter parasites such as cuckoo wasps that appear to “trap-line” nests, visiting them at regular intervals to assess their potential for parasitism. In a brief preliminary trial we presented a nest-associated male with a dead cuckoo wasp glued on a straw. His response was initially to back away to the far side of the nest and then to fly, suggesting that males play little role in nest defense. In other contexts, nest-associated males may provide some deterrent against nest enemies, as we once observed a nest-associated male to lunge at a potential *P. paragioides* nest usurper, causing her to fly off.

Chimney turrets and entrance funnels are constructed by many other solitary nesting vespids, but few are as spectacular as the flared funnel entrance to *Abispa* nests. This downward projecting bell is so conspicuous as to be like a beacon advertising the doorway to a potential bonanza for predators, parasites, and competitors/usurpers able to cue into it. Various hypotheses have been advanced regarding the possible functions of turrets and entrance funnels, but none have been experimentally tested [7]. Our preliminary experiments that confronted females with freshly killed bombyliid and chrysidid parasites showed that the funnel gives *Abispa* females the advantage of blocking the entrance while simultaneously mounting a quick, strong attack upon invaders in a confined arena. While we never observed a nest enemy attempting to walk upon the slippery funnel surface, chrysidids have been observed losing their purchase and sliding down the funnels of a soil-nesting mason wasp, *Paralaster* sp. [15].

We showed that *A. ephippium* females immediately repair and restore damaged funnels (see Figure 10), indicating that the entrance funnel likely plays some important role. Funnel brushing frequency also dramatically increased following our intruder experiments, an observation that strongly hints at an intruder deterrent role for the funnel. Whether the well-developed foretarsal brushes (see Figure 9) apply some substance to the inner surface or simply act to polish it and maintain its smoothness needs further investigation. The discovery that the antennae of certain *Philanthus* wasps (Crabronidae) secrete symbiotic bacteria that inhibit fungus growth [16] suggests another potential area of investigation that might be fruitful.

Although a funnel would provide increased surface area for dispensing chemicals, our experiments with a common local ant species failed to support a chemical deterrence hypothesis. However, as Cowan [7] notes, “the full impact of ants on solitary wasps is probably underappreciated; unlike many other enemies, they may be in a nest for only a short time, and they leave no evidence (such as cocoons) of their visit.” Furthermore, experiments with other nest parasites and predators are needed before we can rule out the existence of possible allelochemical roles in other contexts.

If the funnel were serving primarily to broadcast some deterrent chemical, one might expect it to be left in place at the end of nest construction, even though *Abispa* plugs the entrance hole at its base. However, *Abispa* removes the funnel completely at each cell's completion and builds it anew for each subsequent cell. This observation suggests that whatever the funnel's purpose, it must serve primarily during the interval when the egg has been laid and the cell is being provisioned.

Funnel deconstruction does provide a readily available supply of mud that can be used to close a completed cell rapidly at a very vulnerable stage of nest construction. Collecting this mud at an earlier point in the cell construction cycle entails much lower risk of parasitism, usurpation, and prey theft. Reusing funnel mud for cell closure requires only a few brief water-gathering trips, minimizing and greatly lowering the time (by 77% in our study) that the nest must be left unguarded when the cell is fully provisioned with a developing larva.

Speculating further, we note that humans commonly use funnel-shaped guards above or below bird feeders to thwart squirrels. Lizards have many behavioral and structural features similar to squirrels, so perhaps the funnel functions as a deterrent for lizards or other larger carnivores by making it difficult to insert tongues far enough into the cell to extract prey or larvae. Lizards occurred near nests at our study site, and such predators might be even more common at more natural *Abispa* nesting sites such as within rock crevices.

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