

Use of Communal Nests by Male and Female *Trachypus petiolatus* (Hymenoptera: Sphecidae)

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ABSTRACT: The nesting behavior of *Trachypus petiolatus* is described from central Panamá. Females nested within aggregations in bare soil; they re-used nests from a prior generation, and provisioned their nests with small bees, mainly Apidae and Halictidae. These nests had a communal social organization among resident females, and also included one or more males. At least some males left the nest in the morning on a daily basis, and then returned later in the day. Based on limited nest excavations, we did not observe any parasitized cells, which may be associated with communal nesting.

KEY WORDS: Communal nesting, male behavior, parasites, social tolerance

Howard Evans devoted considerable attention to what he called the “high drama” in the lives of beewolves, *Philanthus* and its relatives (see Evans and O’Neill, 1988). Philanthine wasps include species that sometimes re-use nests, excavate accessory burrows around a functioning nest, and exhibit occasional or regular communal nesting involving multiple females, or females and one or more males. Male beewolves also display a rich diversity of mate-finding and sexual behaviors. Thus, Evans and colleagues realized that comparative studies of the natural history of beewolves would help us better understand the evolution of male mating strategies, and the evolution of social tolerance, among other questions. More generally, such data are also important for understanding how behavioral flexibility promotes or impedes evolutionary change (Evans, 1966b, p. 495ff.; Wcislo, 1989, 2000; West-Eberhard, 2003).

The monophyly of *Trachypus* (Hymenoptera: Sphecidae: Philanthinae) is well supported, and this genus is the sister group to a paraphyletic *Philanthus* (Alexander, 1992). *Trachypus* is distributed from southern Texas in the north, throughout Mexico and the American tropics, and south to Chile; in the tropics *Trachypus* replaces *Philanthus*, which is absent from South America (Rubio, 1975; Bohart and Menke, 1976). Unlike *Philanthus* (see Evans and O’Neill, 1988), the biology of *Trachypus* is not well known, even though these wasps “are deserving of much more attention than they have thus far” (Evans and Matthews, 1973, p. 174; see Hook, 1985). Earlier studies by Janvier [Claude-Joseph] (1928) and others indicate that *Trachypus* females re-use nests within aggregations, and they provision their nests mainly with bees, as do *Philanthus* (e.g., Bertoni, 1911; Bristowe, 1925; Evans, 1964; Callan, 1954; Packer, 1985); *T. petiolatus* (Spinola) in Argentina also used the occasional sphecid and eumenid wasps in addition to the more usual small bees (Evans and Matthews, 1973). Janvier (1928) described nesting behavior of *T. denticollis* Spinola in Chile, and reported that males emerged prior to

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females and then re-entered burrows to mate with emerging females. Subsequently males spent the night in female burrows, often with more than one male per burrow. According to Janvier (1928), when females started to provision cells only one male remained in the nest, apparently functioning like a guard, as known in some other sphecid wasps (e.g., *Oxybelus*) (reviewed in Evans and Matthews, 1973; Rubio, 1975; O'Neill, 2001). In addition to male-female social groups, at least some nests of other *Trachypus* species also contain multiple females, but details of their social behavior are largely unknown (see Bertoni, 1911; Janvier, 1928; Evans and Matthews, 1973; but see Hook, 1985).

Here we present natural history data from a population of *T. petiolatus* in central Panama. Evans and Matthews (1973, p. 174) noted that *Trachypus* wasps "are especially commended to persons living in the tropics who have an opportunity to follow nests over a considerable period of time"—and when wasps were discovered this was the aim of the study. Data are limited, unfortunately, because the nesting site was destroyed by a bulldozer during road maintenance. These limited observations were of interest to Howard Evans (Evans *in litt.* 1996 to WTW) as they confirm findings by Evans and Matthews (1973): females re-use nests from previous seasons, females live together in a communal nest, females switch nests, males regularly cohabit with females in their nests, and nests were free of macro-parasites.

Materials and Methods

Two small nesting aggregations were discovered in hard-packed clay soil, in small bare areas amid grasses and low vegetation along-side an earthen road running through tropical forest near Gamboa (9°07'N, 79°42'W, Colon Province), ~2 km from the Rio Limbo bridge, Pipeline Road, Soberania National Park, Republic of Panama. The earthen road runs through semi-deciduous tropical forest having a mature canopy height up to ~35 m. Mean monthly temperatures are 25–26°C; annual rainfall averages ~2500 mm, with an approximately 4-month long dry season that begins in mid-December or January (meteorological data from the nearby Barro Colorado Island; Windsor, 1990). Nests were first discovered on 12 February 1996. Individual nests were marked with plastic stakes inserted into the soil. Prior to behavioral observations, small transparent plastic cups with a mesh bottom were inverted over nest entrances to capture wasps as they left their nests. Wasps were marked using Testor's™ model paints placed on the thorax; the length (mm) of the right forewings were measured, and then wasps were released. Testor's paint marks usually did not last more than 2 weeks with these wasps, nor did Decacolor™ paint pens, and some wasps had to be recaptured and remarked periodically.

Observations were made at irregular intervals until the end of the dry season in the beginning of May, when activity ceased; wasps were observed on 12 days for a total of 92 person-hours of observations. Nests ($N = 4$) were prepared for excavations by first injecting into each nest a thin slurry of plaster-of-Paris and water, which was allowed to harden; nests were then excavated using a small knife and shovel. Contents of each cell were transferred to the wells of plastic tissue culture trays. Subsequently, for each cell the remains of prey were sorted by body parts that were fixed to small cards with shellac; these reconstructions were used to determine the number (based on head capsules) and identity of prey within cells.

Brief observations were made on two nests in a clear, open area along an earthen road between El Llano (Panama Province) and Carti (Comarca of Kuna-Yala), ~7.5 km N of the Pan-American Highway in March 1996. Vouchers of the wasps and bee prey are deposited in the Dry Reference Collection of the Smithsonian Tropical Research Institute,

Centro Tupper, Ancon, Republic of Panama, and duplicates of the wasps are in the Natural History Museum, University of Kansas, USA.

Results

Nesting Sites

Nests were discovered in two small aggregations at the Soberania site, situated among grass and low vegetation in areas along the side of an earthen road. One aggregation contained 16 nests in a $\sim 1 \times 4$ m area, and a second aggregation measured $\sim 0.5 \times 10$ m and contained 14 nests; two nests were abandoned shortly after the site was discovered. The two aggregations were separated by ~ 15 m. At the Llano-Carti site, two nests were isolated from each other by ~ 12 m, and a thorough search of the area did not reveal any other nests. Unlike the nesting sites of *T. petiolatus* described by Evans and Matthews (1973), the soil did not include appreciable amounts of sand at either site.

Nest Architecture and Nest Re-use

Nest entrances were surrounded by an oblong accumulation of excavated soil (~ 5 – 10 cm in length). There was no evidence that females constructed accessory burrows (see Evans, 1966a). In general, nest architectural features agree closely with those described by Evans and Matthews (1973) for *T. petiolatus* in Colombia. Nest burrows averaged approximately 7 mm in diameter, and entered the soil at a steep angle ($\sim 45^\circ$) to a depth of 20–45 cm, and from there on were roughly horizontal, parallel to the soil surface for 40–178 cm (mean \pm SD tunnel length, 111 ± 57 cm, $N = 4$). The direction of the burrows led toward the road, where the soil must have been more compacted relative to the forest, but we did not systematically measure soil hardness. Nests were evidently re-used from a previous generation, because there were large numbers of old cells along the sections of the burrows nearer to the nest entrances, and there were no indications of a large-scale emergence of wasps during our observations that would account for numerous old cells. These cells contained bee fragments and in some cases empty cocoons. Active cells were found toward the more distant stretches of the horizontal burrows, as if wasps extended the main burrows. The excavated nests contained from 10–35 cells ($x \pm SD = 11.5 \pm 5.8$). Cells were oblong in shape, and were attached to the main burrow with short (~ 2 – 3 cm) lateral burrows. There were no indications that females refurbished and re-used old cells.

Female Nesting Behavior

Females began flying in the morning ($\sim 9:00$), and provisioned their nests with small bees until mid-afternoon (Fig. 1), which roughly corresponds to the period when bees are actively foraging. The duration of hunting trips ranged from 4 to 72 min ($x \pm SD = 16.1 \pm 12.3$ min, $N = 88$). The brief durations of some trips suggest that the wasps did not fly far, but we did not observe wasps hunting on nearby (< 10 m) flowers, where we did observe some of the prey species collecting pollen. Numerous prey had substantial amounts of pollen on their bodies, suggesting that wasps captured bees on flowers, as do other philanthines (e.g., Tinbergen, 1972). When females left their nests some of the loose soil (tumulus) around the entrances slipped and filled in the nest entrances, which were thus closed when females were foraging. After females returned to the nests with prey, they dug through the loose soil with their front legs while they maintained their grasp on the prey beneath their bodies, using their second pair of legs, as described previously (Evans and Matthews, 1973). In some cases the females seemingly could not find their nests, and left

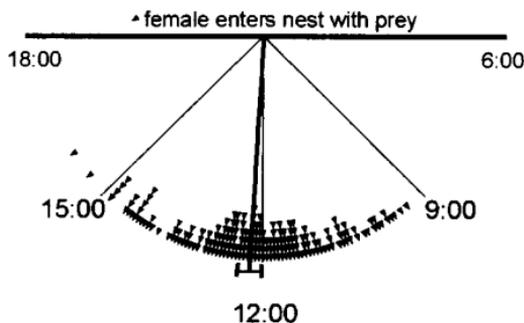


Fig. 1. Diel distribution of nest provisioning activity by female *T. petiolatus* wasps; the thick line represents the circular mean.

prey on the ground, from 1–15 cm from the entrance; when the entrance was finally rediscovered, the wasp then walked or flew to the prey, picked it up, and went directly to the nest and entered it.

Discounting incomplete cells, cells contained from 4 to 13 prey per cell ($x \pm SE = 7.3 \pm 0.34$, $N = 76$ cells) based on head capsules, which is roughly comparable to the number (8–15 bees per cell) reported by Evans and Matthews (1973). The integrity of the prey remains within cells varied considerably, but in all cases could be identified as small to medium sized bees in the Halictidae and Apidae (Fig. 2). Diverse prey species were found in a single cell, suggesting that females did not specialize on a particular prey species.

Nests contained from 2 to 11 females per nest ($x \pm SD = 5.2 \pm 3.2$ females/nest, $N = 9$ nests, excluding all females for which any markings were equivocal so these measures may be underestimates). In all multi-female nests each female was observed bringing prey to the nest. Of 51 females marked while they were actively provisioning a nest, 8 (16%) switched nests and began provisioning in the new nest (Fig. 3), while the remaining wasps continued to use their original nest; this percentage may be an underestimate since a number of possible cases were excluded because of uncertainties with identifying paint-marks. One female consistently drifted from nest to nest, and entered them without carrying provisions, but we never observed her involved with agonistic interactions. Females from two nests ($N = 2$ and 3 females, respectively) were collected and dissected, and all had developed ovaries and sperm in their spermathecae, suggesting that the nesting associations are communal sensu Michener (1974). Overall, females are larger than males (female right forewing length, $x \pm SD = 10.0 \pm 0.6$ mm, $N = 46$; male forewing = 7.4 ± 1.1 mm, $N = 34$), but within nests there were no indications that larger females co-nested with smaller females. Wasps were inactive during the wet season (May–December) at both sites.

Male Behavior

Males usually left their nest tunnels in the morning (~9:00) before females began provisioning nests, and then usually returned at mid-day and re-entered nests (Fig. 4). As for females, when males exited a nest the loose soil from the tumuli partially filled in the entrance, and returning males had to dig their way through to enter. Many males made occasional, very brief (<10 min) forays to the field in the early afternoon, but the reason for these trips was unclear. When females were provisioning, all nests contained at least

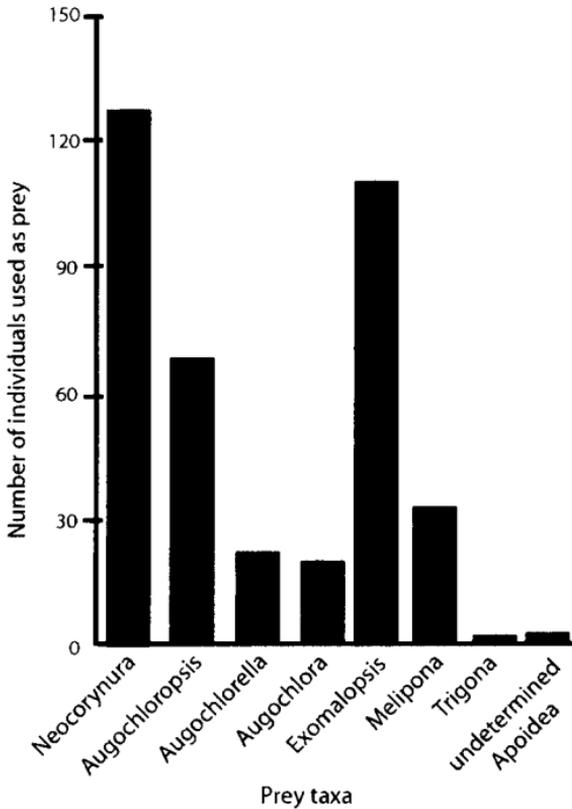


Fig. 2. The numbers of individuals of different bee taxa used as prey by *T. petiolatus* females.

one male, and 7 of 9 nests contained from 2 to 6 males ($\bar{x} \pm \text{SD} = 2.8 \pm 1.5$ males per nest); this estimate excludes all unmarked males, and therefore probably underestimates the number of males per nest. We do not know whether all males exited the nest in the morning, or whether one or more remained behind, as for another *Trachypus* (Janvier, 1928). In two of the excavated nests we recovered 2 and 3 unmarked males, respectively; these observations suggest that some males did not leave the nest, but due to problems with the persistence of the paint marks, the unmarked males could also be those that lost their marks. In no cases were males observed behaving as guards (e.g., by repulsing intruders), but they may nonetheless effectively have behaved as guards if increased activity at the nest entrance reduces the success of parasites. We did not observe any aggressive interactions among males, nor did we observe any signs of sexual behavior between males and females at the nest site.

Parasites and Predators

No cells that had wasp brood contained signs of parasitism, nor did any of the old cells, though the latter often included undetermined fungal hyphae. Adult parasitic flies

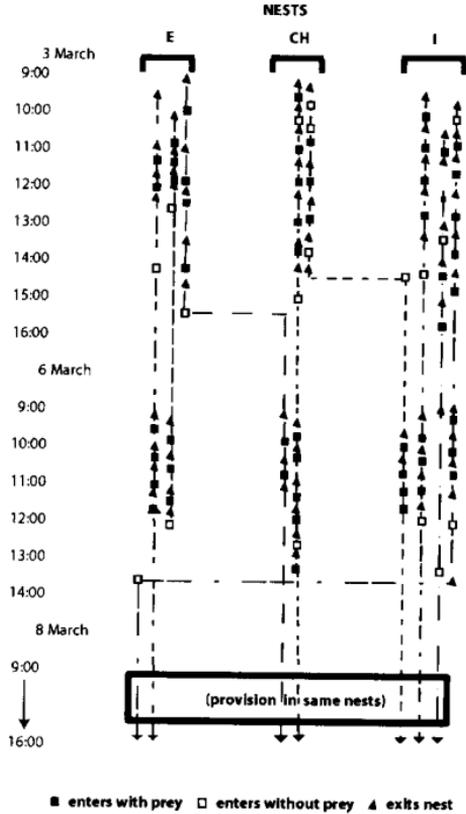


Fig. 3. Representative examples of nest switching by female *T. petiolatus*. Following nest switching, females provisioned in the new nests during the next observation period, although details of foraging activity were omitted for clarity.

(undetermined Bombyliidae) were observed flying at the site, but no fly immatures were discovered in nests at the Soberania site. One adult female aggressively charged out of the burrow at a female *Sphex* (Sphecidae) wasp that attempted to enter the nest, but we did not observe other aggressive interactions by *Trachypus* females. At the Llano-Carti site, a predatory ant, *Ectatomma ruidum* Roger (Ponerinae), hunted prey primarily at *Lasioglossum* bee nests (Halictidae) (see Wcislo and Schatz, 2003), but one ant also entered a *Trachypus* nest and then exited carrying a dead male that presumably it stung inside the nest.

Discussion

The behavior of *T. petiolatus* in central Panama generally conforms to patterns previously described for populations in Colombia and Argentina (Evans and Matthews, 1973), though in all cases observations are based on small numbers of nests. Nevertheless, the data lend additional support to Evans' and Matthews' conclusion that *Trachypus* wasps

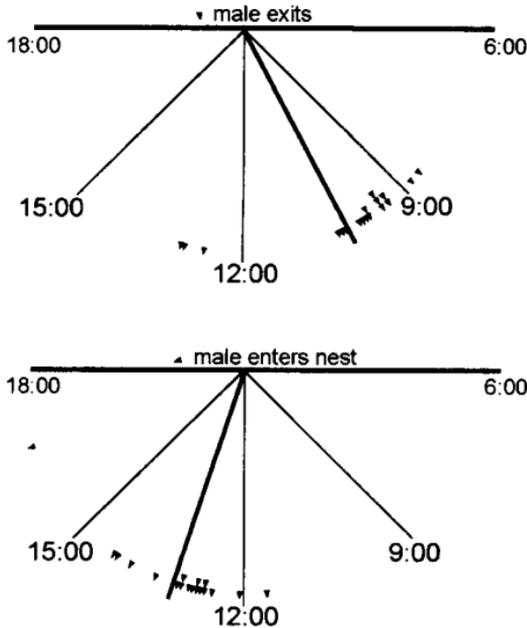


Fig. 4. Diel distribution of flight activity of male *T. petiolatus* wasps. TOP: males exiting nests; BOTTOM: males entering nests. The thick lines represent circular means.

are worthy of more study (also Hook, 1985): they frequently nest in communal social groups involving multiple females and one or more males, and they can re-use nests from a prior generation. Such cross-generational associations of females potentially introduce asymmetries with respect to variables like relative age, size, and residency status, which influence the social control of reproduction. These asymmetries in effect act as environmental changes that can select for the further evolution of division of labor within social groups, as noted by Evans (1966b; Evans and O'Neill, 1988) and others.

Our observations also show that some females switch nests, first provisioning a number of bee prey in a cell in one nest and then subsequently in a cell in another nest. Such nest switching is often associated with examples of nest-sharing in sphecoid wasps, and may be a risk-spreading strategy (e.g., Brockmann *et al.*, 1979; Wcislo *et al.*, 1985; reviewed in Field, 1992; O'Neill, 2001). However, this interpretation is difficult to reconcile with two other observations: i) rates of parasitism were zero, and if this small sample is representative there is little risk to spread (see Evans and Matthews, 1973); and, ii) communal groups themselves are thought to reduce parasitism (see below), again implying there is less risk to spread.

Our limited data suggest that wasps are active only during the dry season, which is when many solitary or weakly social bees are most active in central Panama, while stingless bees are active nearly the year round (Roubik, 1989; WTW, unpubl. data). Since wasps hunt the latter as prey, presumably it is abiotic factors such as rainfall that limit their ability to excavate cells or obtain sufficient prey within rain-free periods. In our samples the two most common prey were *Neocorynura* (Halictidae) and *Exomalopsis* (Apidae) (Fig. 2), but

wasps did not specialize on a given prey species, as inferred from finding diverse prey within single cells. In central Panama nests of both of these bee genera are difficult to find, and they are rarely the most abundant bees on flowers (WTW, pers. obs.); these subjective impressions on relative abundance are supported by quantitative surveys of bee diversity and abundance elsewhere (e.g., Laroca *et al.*, 1982).

Although some females apparently re-use nests, we had no indications that females re-use cells, unlike some communal wasps such as the spider-wasp, *Auplopus semialatus* Dreisbach (Wcislo *et al.*, 1988). The fact that nest burrows of *Trachypus* are quite long (and thus presumably costly to dig in hard-packed soil) may help explain why nest re-use is advantageous. We did not measure soil hardness, though subjectively excavations were difficult for us; Evans and Matthews (1973, p. 166) also commented on their "struggles [in excavating] . . . the deep and complex nests" in Colombia.

Evans and Matthews (1973) showed that *T. petiolatus* nests in Argentina and Colombia suffered no losses from parasites and predators, and these authors speculated that the low susceptibility to parasites may be associated with the co-occurrence of group-nesting. Our equally limited nest excavations provide another population of *T. petiolatus* nests that was free of macroparasites, which lends further weight to their suggestion. Such an advantage against parasites would create conditions that favor further evolution of social tolerance, as Evans (e.g., Evans and O'Neill, 1988) and others have suggested (e.g., Moynihan, 1998; Wcislo, 2000; Melo, 2000). Likewise, cohabitation of males and females may also be advantageous in reducing parasitism. In the latter case, presumably any defense is passive, being derived from the male's physical presence, rather than any defensive behavior, since males lack useful weapons (stings or enlarged mandibles). However, to again refer to Evans and Matthews (1973), all these aspects of their behavior need longer term studies to fully address them.

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