

Behavior notes and prey spectrum of three species of the bee-hunting wasp *Trachypus* Klug (Hymenoptera: Apoidea)

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Abstract. *Trachypus* Klug is a Neotropical genus of crabronid wasps comprising 31 ground-nesting species. Its species can be solitary or communal, and two diet ranges are known: they can forage on several bee subfamilies and wasps; or can be specialists on stingless bees. Natural history observations are scarce nowadays but are essential to contextualize ecological and evolutionary studies. Here we report new records and give biological notes for *Trachypus elongatus* (Fabricius, 1804), *Trachypus taschenbergi* Rubio-Espina, 1975, and *Trachypus varius* (Taschenberg, 1875). Observations and samplings were carried out twice a month, during one year in the city of Curitiba, southern Brazil. Besides field observations, circular statistics were used to analyze seasonality. All species nest in sloped soil and are solitary. *Trachypus elongatus* and *T. taschenbergi* were active during most of the year with marked seasonality in the late spring and early summer. Both species were observed hunting only stingless bees, with *T. elongatus* specialized on *Trigona spinipes* (Fabricius, 1793), and *T. taschenbergi* specialized on *Paratrigona subnuda* Moure, 1947 drones. *Trachypus varius* was observed only in January and one female was recorded foraging on a *Paratrigona subnuda* worker. Our observations provide additional data for understanding the biology of bee-hunting wasps, and this is the first study to bring information for *T. taschenbergi* and *T. varius*. Our data corroborate that some species of the genus *Trachypus* are specialized on stingless bees.

Keywords. Digger wasp; Foraging; Nesting biology; Predator-prey; Seasonality.

INTRODUCTION

Trachypus Klug, 1810 (Hymenoptera: Apoidea: Crabronidae: Philanthinae) comprises ground-nesting wasps that hunt bees and more rarely other wasps (Evans & Matthews, 1973; Rubio-Espina, 1975; Polidori *et al.*, 2009). The genus was revised by Rubio-Espina (1975) and currently comprises 31 species restricted to the Neotropical Region (Amarante, 2006; Pulawski, 2019). *Trachypus* is a monophyletic group nested within the paraphyletic *Philanthus* Fabricius, 1790 as suggested by Alexander (1992) using morphology, and later by Kaltenpoth *et al.* (2014) and Sann *et al.* (2018) using molecular data. Rubio-Espina (1975) recognized *Trachypus* as a separated genus from *Philanthus* supported mainly by: first metasomal segment petiolate in both sexes, and last antennal flagellomere strongly truncated. The *Philanthus* paraphyly demands further genus descriptions to make natural the classification of its clade.

Natural history information is available in the literature for nine species: *Trachypus bohar-*

ti Rubio-Espina, 1975 (Giannotti & Pinto, 2001; Koedam *et al.*, 2009, 2011), *Trachypus denticollis* Spinola, 1851 (Janvier, 1928; Polidori *et al.*, 2009), *Trachypus elongatus* (Fabricius, 1804) (Bristowe, 1925), *Trachypus fulvipennis* (Taschenberg, 1875) (Buys, 2016), *Trachypus gracilis* (Cameron, 1890) (Packer, 1985), *Trachypus mexicanus* de Saussure, 1867 (Evans, 1964; Menke, 1980), *Trachypus patagonensis* (de Saussure, 1854) (Bertoni, 1911), *Trachypus petiolatus* (Spinola, 1842) (Evans & Matthews, 1973; Menke, 1980; Callan, 1990; Wcislo *et al.*, 2004), and *Trachypus romandi* (de Saussure, 1854) (Bertoni, 1911). In summary, most species are solitary with some reports of communal behavior. About their diet, some species forage on several bees and wasps groups while others are specialized on stingless bees.

This study provides biological notes for three *Trachypus* species: *Trachypus elongatus* (Fabricius, 1804), *T. taschenbergi* Rubio-Espina, 1975, and *T. varius* (Taschenberg, 1875). *Trachypus elongatus* occurs from Ecuador to southern Paraguay, and there are two records from Paraná State, Brazil

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(Rubio-Espina, 1975; Pulawski, 2019). Some aspects of this species were previously observed by Bristowe (1925). *Trachypus taschenbergi* occurs from southeastern Brazil to Argentina; in Paraná it was recorded around 50 km north of Curitiba (Rubio-Espina, 1975). From the examined material in Rubio-Espina (1975) revision there is one specimen of *T. varius* previously known from Curitiba. This is the first study bringing natural history information for the latter two species.

MATERIAL AND METHODS

Nesting aggregations of these wasps were found in an urban site in Curitiba, Paraná Sate (southern Brazil) during a monitoring program on bees' nests. The study area consists of a series of street side earth banks (1,130 m of extension, ranging from one two meters of height), sloped 30° to near vertical exposed soil after the road cutting (Michener *et al.*, 1958). This area is located at Parque Barigui, an urban amusement park (25°25'22.2"S, 49°18'30.7"W; 905 m), in Curitiba, Paraná State, Brazil (Fig. 1A). Natural plant cover in this city region is a mix of *Araucaria* forests, wetlands and natural grasslands within the Atlantic Forest ecoregion. The climate is subtropical (average temperature, summer – 22°C, winter – 17°C, average rainfall – 1,480 mm; INMET – Instituto Nacional de Meteorologia). Besides the square park, with remnants of natural vegetation, there are several residential buildings and paved roads in surroundings (Fig. 1B), with 56% of landcover composed by impervious surfaces (Pereira *et al.*, 2020).

Michener *et al.* (1958) studied bees in this area in 1955, investigating abiotic factors influencing the distribution of ground-nesting bees and the authors originally delimited 492 contiguous sites (under their terminology of "divisions") of 3.5 meters each (Fig. 1C). The same site delimitation was used by us to monitor the bee assem-

blage in a separate study (Pereira *et al.*, 2020). The same sampling design was used in this study. The nesting sites were monitored for one entire year (June 2018 – June 2019), twice a month, during the time of highest wasp activity (9 AM to 3 PM), and restricted to days with warm temperatures and no rainfall (> 20°C). Specimens were occasionally collected with insect nets, when entering the nests or patrolling aggregations sites, for identification in the laboratory. Females returning to their nest after a provisioning flight were intercepted to collect preys. We identified the wasps at the genus-level with the key provided by Menke & Fernández (1996), and to species-level following the revision of Rubio-Espina (1975). The bees were identified at genus-level following Silveira *et al.* (2002), and species were identified with specimen comparison in Padre Santiago Moure Entomological Collection (DZUP, Federal University of Paraná), where all voucher specimens from this study are deposited. Some females were marked with blue and yellow paint marker pens (Uni Posca®) in order to investigate nest sharing.

Circular statistics was used to test whether seasonal activities were evenly distributed throughout the year, considering the number of female observations for each species in each month. Here, the months were treated as sectors of 30° each, with January beginning at 0° and December at 330°. We did not include *T. varius* due to the small number of observations (n = 9). For other species we calculated the circular standard deviation (sd), circular mean (in degrees), and the length of the vector (r) – that ranges from 0 (abundance evenly distributed throughout the year) to 1 (abundance totally concentrated in a period of the year) (Morellato *et al.*, 2010). Then, a Rayleigh test (Z) was applied to test the significance of the circular mean, where p < 0.05 states that the circular mean is significant and, therefore, we assumed as a seasonal pattern (Morellato *et al.*, 2010). All circular statistics analyzes were conducted using the software Oriana version 4.2 (Kovach, 2011), also used to plot rose diagrams

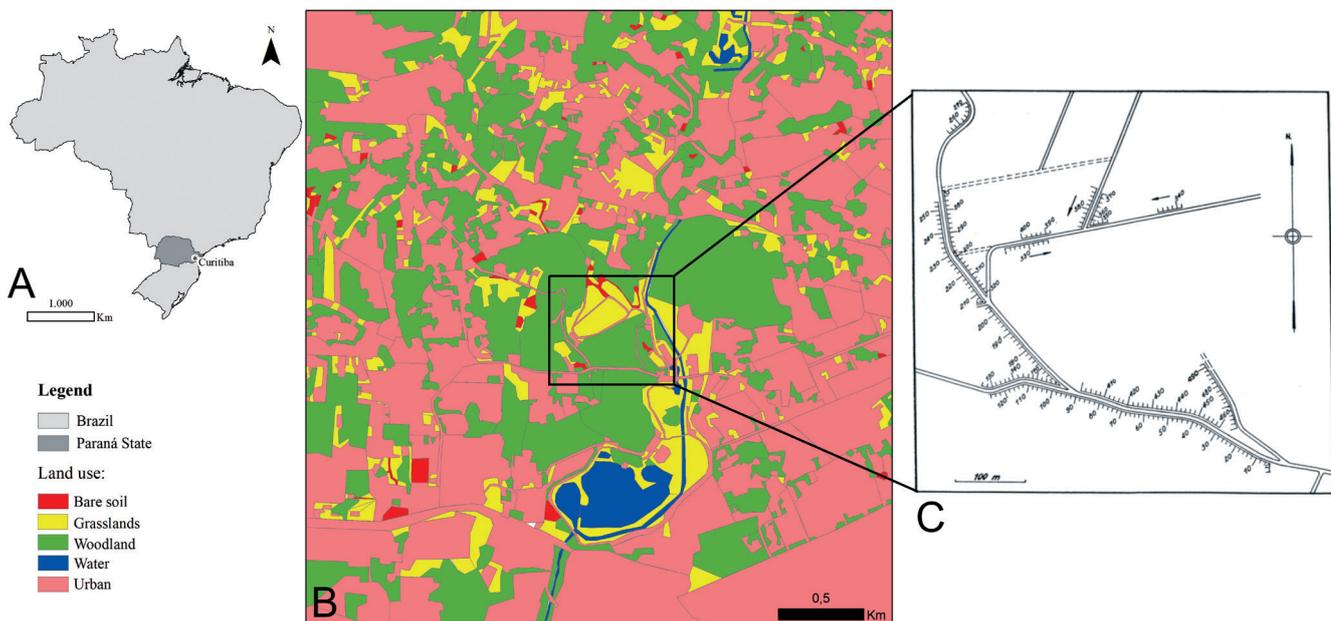


Figure 1. Study site. (A) Curitiba, Paraná, Brazil, (B) land cover (modified from Pereira *et al.*, 2020), (C) original sampling sites (modified from Michener *et al.*, 1958).

for species seasonal activities. The rose diagrams and other figures were edited in Inkscape (version 1.0) and GIMP (version 2.10.12).

RESULTS

Trachypus elongatus (Fabricius, 1804)

We found a sum of 24 nests distributed in seven divisions: 86 (n = 2); 88 (n = 5); 91 (n = 2); 92 (n = 7); 97 (n = 5); 198 (n = 1); 416 (n = 2). Nests in divisions 86 and 88 were located in a part of the bank exposed to the sun in the morning and partially covered in the shade from a bus stop in the afternoon. Those in divisions 91, 92, and 97 were continuously exposed to sunlight all day, while in 198 and 416 were in banks predominantly covered by shadows from trees. The latter was on soil with higher humidity from dew. Females were active from November to March (late spring and summer). Circular statistics revealed a non-uniformly abundance distribution along the year, a significant seasonal pattern (n = 72 observations; p < 0.05, Rayleigh (Z) test) was found with the mean vector in December (Table 1; Fig. 2A). Males were observed only in December 2018, flying over the nest sites, but no mating behavior was observed.

Nest excavations by the wasps stopped around 1 PM, then each female stayed in its respective nest and exhibited guard behavior, with the following female patterns: (i) closing the nest entrance with its head; (ii) exposing its head outside the entrance and opening its jaws whenever another individual (same species or not) appeared near the nest. Defense behavior (iii) occurred more frequently against *T. taschenbergi* females that tried to enter the nest and then immediately retreated, without

Table 1. Circular statistics results of seasonal activity data, considering the total number of female observations. Number of observations (females), mean vector (in degrees), length of the vector (r), circular standard deviation (sd), and Rayleigh test (Z) statistics result. The (*) in Rayleigh test (Z) results represent p < 0.05 (1E-12 in both cases).

Species	Observations	Mean vector	Length of the vector (r)	sd	Rayleigh test (Z)
<i>T. elongatus</i>	72	351.87°	0.741	44.315°	39.586*
<i>T. taschenbergi</i>	395	327.09°	0.440	73.439°	74.401*

conflict. No evidence of two or more females sharing the same nest was observed. Foraging and provisioning activities were observed from November until March. In one case, a female left the nest and returned more than 30 minutes later with a prey. In total, we sampled seven prey items, six workers and one drone of the stingless bee *Trigona spinipes* (Fabricius, 1793).

Trachypus taschenbergi Rubio-Espina, 1975

Trachypus taschenbergi was the more abundant and spread species in the study area. We found a total of 87 nests distributed in 18 divisions: 68 (n = 2); 71 (n = 1); 86 (n = 8); 87 (n = 13); 88 (n = 7); 89 (n = 1); 90 (n = 2); 91 (n = 3); 92 (n = 24); 94 (n = 4); 160 (n = 5); 197 (n = 2); 198 (n = 3); 211 (n = 1); 212 (n = 2); 262 (n = 3); 416 (n = 3); 452 (n = 4). In divisions 68 and 71 the nests were predominantly covered by shadows from trees above the earth bank, but exposed to sunlight in early afternoon (around 12 noon to 2 PM). Those in divisions 86-88 were located in a part of the earth banks predominantly exposed to sunlight throughout the day and with a portion partially covered by the shade from a bus stop in the afternoon.

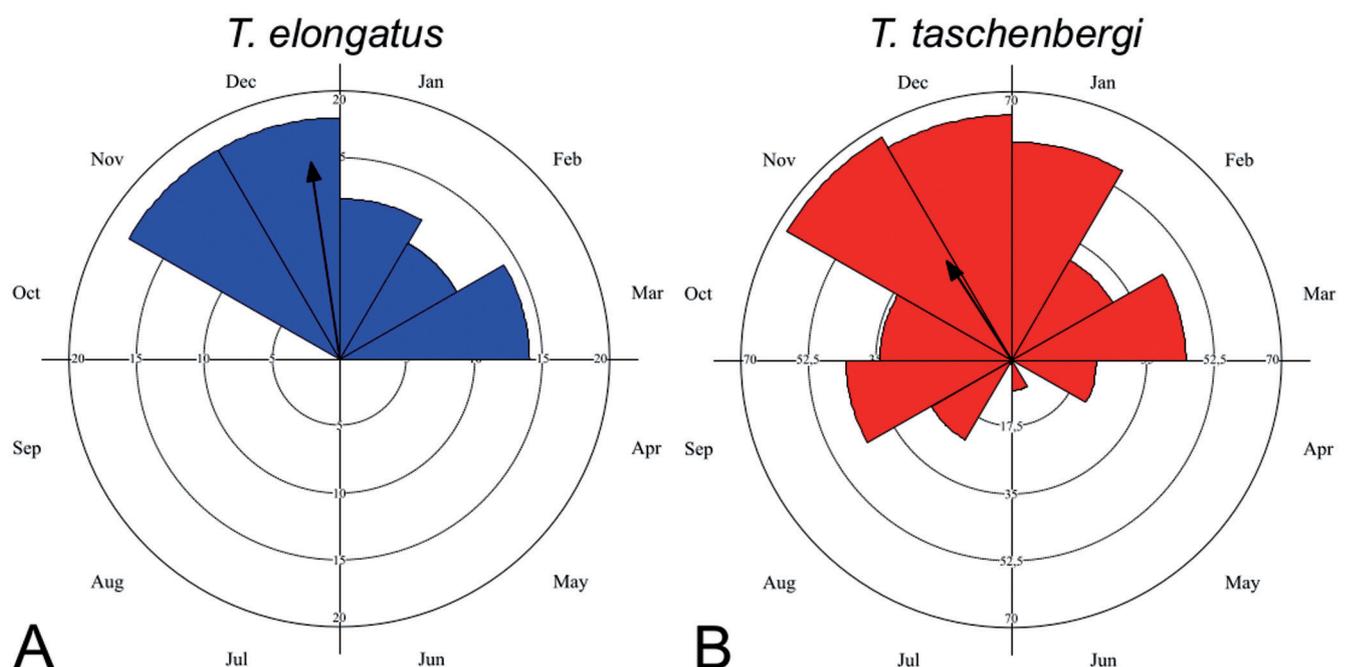


Figure 2. Rose diagrams for seasonal activities of (A) *Trachypus elongatus* and (B) *Trachypus taschenbergi*, considering the number of female observations per day of fieldwork. Months are treated as sectors of 30 degrees each, with January corresponding to 0 and December to 330.

Nests in 89-94, 160, 211 and 212 were exposed to sun throughout the day, while in 197, 198, 262, 416 and 452 were constantly in the shade.

Females were active during the entire year, including the winter season, we observed few females excavating nests in June 2018 (n = 5) and in August 2018 (n = 3). Activity was not detected in May 2019, a very rainy month, but in June 2019 a few females were observed. Circular statistics revealed a non-uniformly abundance distribution along the year and a significant seasonal pattern (n = 395 observations; $p < 0.05$, Rayleigh (Z) test) was found with the mean vector in November (Table 1; Fig. 2B). Males were observed from September to March. They were more abundant on October and January (spring and summer).

The foraging activities started after 9 AM, usually with females opening the nests between 9h30 AM and 10h30 AM. As in *T. elongatus*, nest construction and provisioning rarely continued until after 2 PM. Females exhibited guarding behavior, very similarly to *T. elongatus*, by exposing its head and opening its mandible when another individual tried to enter in its nest. A marked female was observed entering nests and in one case, the female stayed a few minutes inside a nest and then was expelled by a resident female. Later, the same marked female entered another burrow and stayed inside, expelling other females that tried to enter. No evidence of two or more females sharing the same nest was observed. Activity of males near to the nesting sites occurred in the afternoon, when the females were guarding the nests. The males flew in aggregations of 10-20 individuals, in which one at time tried to enter a nest, while the females expelled the male by exposing its head and opening its mandible. After a while (about 30 minutes) the female allows one male to enter the nest and keep protecting the entrance. Presumably, copulation occurred inside the nest, no mating was observed near the nesting sites.

Provisioning activities were detected from September to April. The observed prey spectrum showed a strong preference for drones of *Paratrigona subnuda* Moure, 1947, only one worker was recorded (n = 59 preys). The foraging trips usually took less than five minutes of duration. We observed a female exiting the nest and returning in less than two minutes with a prey and three minutes later she left the nest again. A marked female provisioned her nest four times in a period of 15 minutes. On the other hand, we observed a foraging trip that lasted 30 minutes. Whenever arriving carrying a prey, a female spent time flying over the nesting area, looking for its nest, and landed near the entrance (Fig. 3A) entering quickly. When a female carrying a prey was prevented by us from entering the nest (with a stick or the insect net), she immediately dropped and abandoned the prey, returning a few minutes later with a new prey.

***Trachypus varius* (Taschenberg, 1875)**

We found nine nests distributed in three divisions: 97 (n = 1); 128 (n = 3); 129 (n = 5). The isolate nest in divi-

sion 97 was near to a small aggregation of *T. elongatus* (n = 5). Females of this species were observed only in January 2019, in the nest provisioning activity. A male was observed once in January, but an additional male was sampled in November 2017 in an isolated record. We only sampled one female carrying a worker of *P. subnuda*.

DISCUSSION

Nest abundance and behavior

We found a total of 120 bee hunter nests with three species co-occurring in many sites. *Trachypus taschenbergi* was the most common species followed by *T. elongatus*, while *T. varius* was represented by only nine nests. The nests are in sloped soil as commonly found by other species of the genus (Polidori *et al.*, 2009). Despite nesting aggregations occurring in several sampling divisions, we found no evidence of cooperation: all observed interactions were hostile. However, further studies with marked nests and more fine observations would provide reliable observations and evidences about intraspecific interactions. Wcislo *et al.* (2004) reported communal behavior for *Trachypus petiolatus* from Panamá, with reuse of nests among generations. These differences suggest that *Trachypus* nesting behavior and also the prey spectrum as discussed below, are variable among its species. We did not observe mating near nesting sites, but observations suggest that copulation may occur inside the nests. Males spending the night at nests guarding the nest entrances are known for *Trachypus denticollis* and *T. petiolatus* (Wcislo *et al.*, 2004; Polidori *et al.*, 2009). For both *T. taschenbergi* and *T. elongatus* we observed a weak preference for nesting on soil exposed to sunlight; however, both species we also found on shadowed surfaces.

Seasonal activity

Our results indicated that *T. elongatus* and *T. taschenbergi* have seasonal activities in the late spring (November and December) during the studied year. However, for both species the activity period lasted several months (especially for *T. taschenbergi*) indicating that the populations could be multivoltine in the study site. As they hunt eusocial bees with perennial activity, food is available the entire year despite the lower density of Meliponini during winter time. Even specializing on drones, *T. taschenbergi* can benefit from the biology of *P. subnuda*, due to the numerous male production by worker caste. On average 64% of *P. subnuda* males are produced by such caste (Tóth *et al.*, 2002), greatly increasing the number of male offspring. The third species, *T. varius*, was sampled only once in the year and the small population did not allow us to infer about its activity.

Trachypus denticollis activity in Chile was investigated only for a short period of the year, from December until February (Janvier, 1928; Polidori *et al.*, 2009). Wcislo *et al.* (2004) observed *Trachypus petiolatus* in Panama

from February until May, when activities ceased, similarly to what we found in this study for *T. elongatus* and *T. taschenbergi*. The other studies were based on observations of a few days during the summer (Evans & Matthews, 1973; Menke, 1980; Koedam *et al.*, 2009; Buys, 2016). The present study is the first to investigate the seasonal activities of *Trachypus* species during a entire year, what helps to explain the broader temporal range when compared to the previous data.

Prey spectrum

Available prey records in the literature suggest two different patterns: (i) some species hunt on a wide variety of bees, and also prey wasps (Evans & Matthews, 1973; Menke, 1980; Wcislo *et al.*, 2004; Polidori *et al.*, 2009); (ii) some species are specialized on stingless bees (Koedam *et al.*, 2009; Buys, 2016). Even with the presence of some species of Colletinae and Halictinae bees in the

same nesting sites (Pereira *et al.*, 2020), the *Trachypus* species studied in this site only hunted the stingless bees. Michener *et al.* (1958) did not mention *Trachypus* nor Meliponini bees in the study site, thus this could indicate a more recent colonization.

The same predator-prey association between *Trachypus elongatus* and *Trigona spinipes* was previously recorded by Bristowe (1925) in Rio de Janeiro, Brazil, suggesting a specialization. *Trigona spinipes* is a very common species in Brazil, which increased its abundance and distribution with the urbanization in Curitiba as well in other disturbed environments (Martins *et al.*, 2013; Cardoso & Gonçalves, 2018). Thus, localities with the presence of *T. spinipes* can also harbor populations of *T. elongatus* if other biological requirements are matched, such as availability of proper nesting substrates.

Prey spectrum restricted to drones of stingless bees was previously observed for *Trachypus boharti*, which preys on males of *Scaptotrigona postica* (Giannotti & Pinto, 2001; Koedam *et al.*, 2009). Koedam *et al.* (2009,

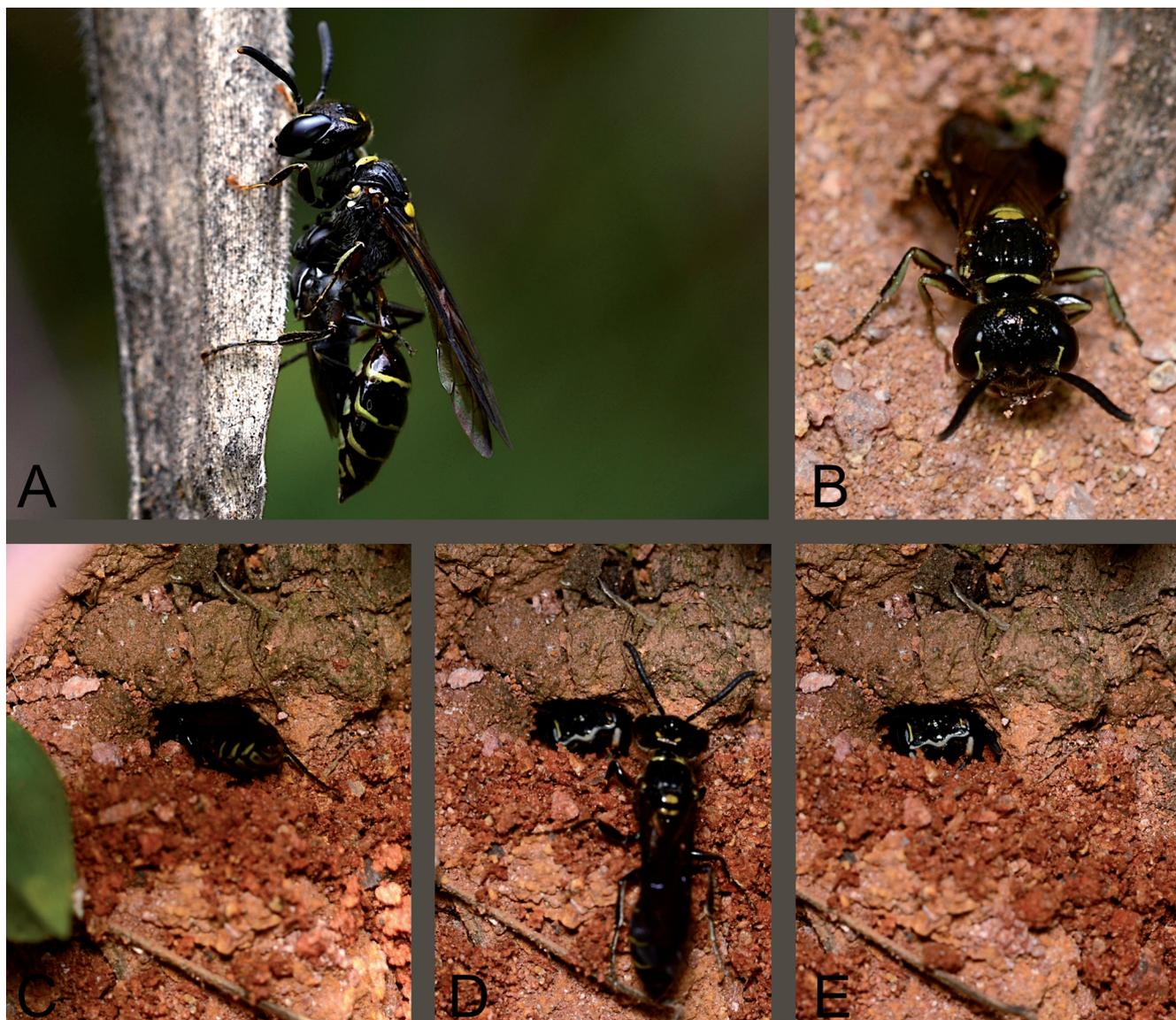


Figure 3. *Trachypus taschenbergi* biology. (A) female carrying a prey (*Paratrigona subnuda* drone) near the nest entrance. (B) female exiting the nest; (C-E) a female trying to enter an occupied nest and being expelled by a female that was inside the nest.

2011) found that the attacks occur near the colony entrances, once drones of *Meliponini* tend to congregate in clusters near nests, waiting for new queens initiating their nuptial flight (Roubik, 1990; Sommeijer & de Bruijn, 1995). We presume that a similar mechanism may occur with *T. taschenbergi*. We found three *Paratrigona subnuda* nests near the wasps' aggregations (Pereira *et al.*, 2020) and this is the most common species nearby the study site (unpublished data). The nest density of this species can be surprisingly high; Mouga (2014) found a density of almost 2.5 nests per hectare in another site in São Paulo, Brazil.

O'Neil & Evans (1982) observed four sympatric species of the beeswolves *Philanthus* nesting in close proximity, with moderate overlap of nesting sites and low niche overlap in prey kind and size. We observed a low overlap of nesting sites between *T. elongatus* and *T. taschenbergi* in a few sites. The sympatric occurrence of closely taxonomic related species in the study of O'Neil & Evans (1982) is explained mainly by the differences in prey choices. In the present study, there is no overlap in prey species of the two most abundant species, an observation probably associated with different body size between both species.

CONCLUSION

We studied *Trachypus elongatus*, *T. taschenbergi*, and *T. varius* during one year, observing that nests are excavated in sloped soil by solitary females without communal behavior. The nest aggregations of *Trachypus elongatus* and *T. taschenbergi* were active during several months with marked seasonality in the late spring and early summer. Also, both species were observed hunting only stingless bees, with *T. elongatus* specialized in *Trigona spinipes*, and *T. taschenbergi* specialized in drones of *Paratrigona subnuda*. Few females of *T. varius* were observed nesting in January and one female was sampled carrying a *P. subnuda* worker. Studies with natural history observations are scarce in the modern literature but are essential to contextualize ecological and evolutionary studies. Our study brought additional data to understand the biology of bee-hunting wasps, being the first report for *T. taschenbergi* and *T. varius*. Also, the presented data reinforces that some species of *Trachypus* are specialized in stingless bees, while communal species of the genus are generalist on several bees and wasps lineages.

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AUTHORS' CONTRIBUTIONS

F.W.P: Conceptualization, data collection, investigation, analysis, writing. R.B.G.: Supervision, conceptualization, data collection, investigation, writing. No potential conflict of interest was reported by the authors.

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