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Observations on the urban ecology of the Neotropical stingless bee *Tetragonisca angustula* (Hymenoptera: Apidae: Meliponini)

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Abstract. *Tetragonisca angustula* (Latreille) is a small, docile, cavity-nesting stingless bee that is widely distributed in the Neotropical region. This species is particularly abundant in disturbed environments, including human settlements. Between August 2005 and March 2006, we located and followed during eight months 59 nests of this species in Medellín, the second most populated city in Colombia. Herein, we document their foraging behavior, mortality, and incidence of predators and natural enemies. Also, to determine if higher ambient temperature and light intensity in urban environments affect the daily foraging activity of *T. angustula*, we compared the daily foraging activity of bees from nests found in open areas in the city and bees from nests from a nearby covered, forested area. Likewise, to determine if urban nests of *T. angustula* are largely undetected and undisturbed by people, we experimentally made them visible by adding a ring color (white, red, or black) around the nest entrance tube. Our observations indicate that higher ambient temperature and light intensity in urban environments do not significantly affect the daily foraging activity of *T. angustula*. Nearly half of the marked nests disappeared, thus suggesting that nests of *T. angustula* are often undetected by people in Medellín. We discuss briefly some features of the biology of *T. angustula* that might contribute to its success in urban environments.

INTRODUCTION

In general, relatively little is known about the ecology of arthropod communities living in urban environments, which shows the lack of attention to and opportunities available for research in this field (*e.g.*, McIntyre, 2000). Biotic (food sources, preda-

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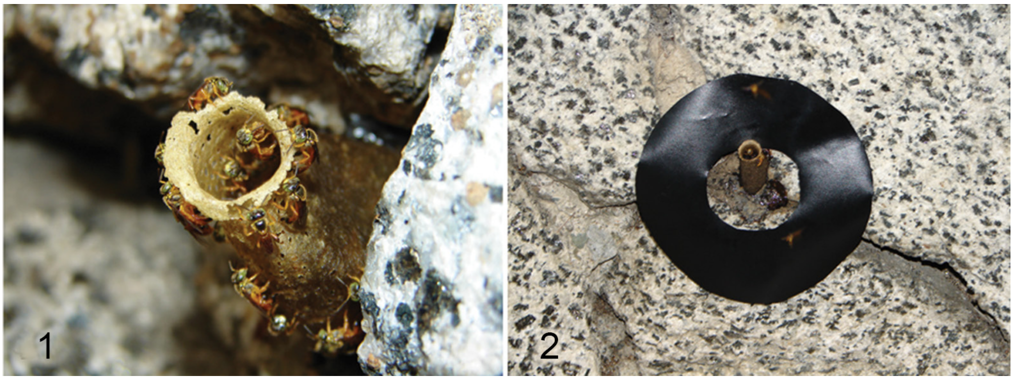

Figures 1–2. Nest of *Tetragonisca angustula* (Latreille) in the city of Medellín, Colombia. **1.** Unmarked nest. **2.** Marked nest with black ring to make the nest more visible to people.

tors, parasites, *&c.*) and abiotic (light, temperature, humidity, *&c.*) conditions in urban settings are significantly different from those in rural or forested areas. For example, cities are known as "heat islands" because they are often warmer due to an increase of heat production from the concentration of people and machines as well as increased heat reflectance and absorbency from pavement (Kim, 1992). Urban conditions may favor the establishment of some species while preventing the same in others.

Among synanthropic stingless bees, or species co-habiting with human populations, *Tetragonisca angustula* (Latreille) is perhaps the most common and abundant (*e.g.*, Sousa *et al.*, 2002; Batista *et al.*, 2003; Nates-Parra, 2005; Slaa, 2006; Nates-Parra *et al.*, 2008; Rasmussen & Gonzalez, 2009). This minute (~5 mm in length), yellowish species lives in small colonies (<5000 individuals) within pre-existing cavities in the ground, tree trunks, or associated with diverse types of human constructions (*e.g.*, Schwarz, 1948; Vergara *et al.*, 1986). Nests are entirely built inside the cavity, except for the entrance tube made of perforated, pale wax (Fig. 1). *Tetragonisca angustula* ranges from southern Mexico to Brazil and it is presumably composed of several undescribed species. The 'true' *T. angustula* might be restricted to Brazil, as it was described from a worker collected in that country and whose whereabouts are unknown (*cf.* Camargo & Pedro, 2007). Unlike other synanthropic stingless bee species, such as some in the genera *Partamona* Schwarz and *Scaptotrigona* Moure, that aggressively attack human or large vertebrate intruders, workers of *T. angustula* usually retreat inside the nest (*e.g.*, Nates-Parra & Cepeda, 1983). However, *T. angustula* is known for its sophisticated defense system against robber bees of the genus *Lestrimelitta* Friese, which involves two complementary, morphologically specialized groups of guards (*e.g.*, Grüter *et al.*, 2011; Grüter *et al.*, 2012). Honey, pollen, and wax of *T. angustula* are highly valued in many regions across Latin America because of their attributed medicinal properties (*e.g.*, Nates-Parra, 2005; Ayala *et al.*, 2013).

Although a number of papers regarding the ecology and natural history of *T. angustula* in natural environments are available (*e.g.*, Vergara *et al.*, 1986; Nates-Parra & Cepeda, 1983; Roubik, 1983, 1989), relatively little is known about its ecology in urban conditions. As an attempt to gain a better understanding of the ecology of *T. angustula* in the city of Medellín, we addressed the following questions: Do higher ambient temperature and light intensity in urban environments have an effect on the daily foraging activity of *T. angustula*? Are nests of *T. angustula* in urban environments largely undetected by people? What is the mortality rate of *T. angustula* in an urban environment?

MATERIAL AND METHODS

Observations were made between August 2005 and March 2006 in the city of Medellín (1479 m), Department of Antioquia, Colombia. A total of 59 nests of *T. angustula* were located at the following sites within the city: 1) Botanical Garden 'Joaquín Antonio Uribe', 2) Universidad de Antioquia, 3) Universidad Nacional de Colombia, and 4) Cerro El Volador (Ecoparque municipal). All of these areas are generally characterized by having a mixture of remnant patches of native vegetation, planted gardens, and landscaped yards. The location, height above ground (measured to base of entrance tube), and length and diameter of the entrance tube were recorded for each nest.

To determine if higher ambient temperature and light intensity in urban environments have an effect on the foraging activity of *T. angustula*, we established and compared the daily foraging activity of bees from four nests, one from each urban area, with two nests found in the Reserva San Sebastián, a nearby forested area. The two nests in the forested area were located for comparison purposes only; no additional efforts were made to find other nests in this forest. All observed nests were found at a similar height above ground but differed in the degree of exposure to sunlight and ambient temperature and humidity (Table 1). Every 30 minutes, for a period of five minutes, we recorded the number of workers entering each nest during two consecutive days in January and March, 2006. We also recorded the ambient temperature, relative humidity, and light intensity in shade using a digital hygrothermometer (Extech Easyview Hygro-Thermo), and luxometer (Extech EasyView Light Meter).

We hypothesize that nests of *T. angustula* are largely undetected and undisturbed by people in urban environments because they are built inside pre-existing cavities and the only visible structure is the pale, soft, entrance tube. To test this hypothesis, we made nest entrances more visible by adding a colored ring around the entrance tube. These rings were made of white, red, or black paper of about 11 cm in diameter (Fig. 2) and were randomly assigned to three nests on each of the four localities. Rings were set up at night when bees were not foraging and people were not around. We used unmarked nests as control. In addition, to test for the effect of these marks on the guarding behavior of the bees, we compared the number of workers hovering in front of a marked nest entrance with those unmarked.

To determine nest mortality, we recorded the presence or absence of each nest according to a monthly census during the eight month duration of the study. A nest was recorded as active when bees were observed entering and leaving the entrance tube. Damage to the entrance tube or to the colored rings was recorded and assumed as a result of being detected.

To test the effect of ambient temperature, relative humidity, and light intensity on the number of foraging bees we used a multiple linear regression. We used a one-way ANOVA to test the effect of the colored rings on the number of foragers hovering in front of the nest entrance and to detect differences in the average number of bees entering the nests between the nest located in the city and in the forest. Mean values are given with standard deviation. Voucher specimens were collected for future taxonomic analyses and are deposited in the Museo Entomológico Francisco Luis Gallego, Facultad de Ciencias, Universidad Nacional de Medellín, Medellín, Colombia.

Table 1. Study sites in the city of Medellín, Deparment of Antioquia, Colombia, and nearby forested area where nests of *Tetragonisca angustula* (Latreille) were found. For light intensity, minimum and maximum averages values are provided.

Study sites	# nests	Coordinates	Average ambient temperature (ºC)	Average relative humidty (%)	Light intensity (Lux)
City of Medellín					
Universidad Nacional de Colombia	24	6º15.667N, 75º34.693W	23.7	62	51.4–6884
Universidad de Antioquia	24	6º15.696N, 75º34.070W	23.9	63	18–2642
Cerro El Volador	4	6º15.874N, 75º34.962W	23.6	62	22.3–4155
Botanical Garden 'Joaquín Antonio Uribe'	7	6º16.306N, 75º33.775W	22.6	59	40.8–7620
Forested area					
Reserva San Sebastián	2	6º6.976N, 75º32.593W	18.2	72	19.1–3208

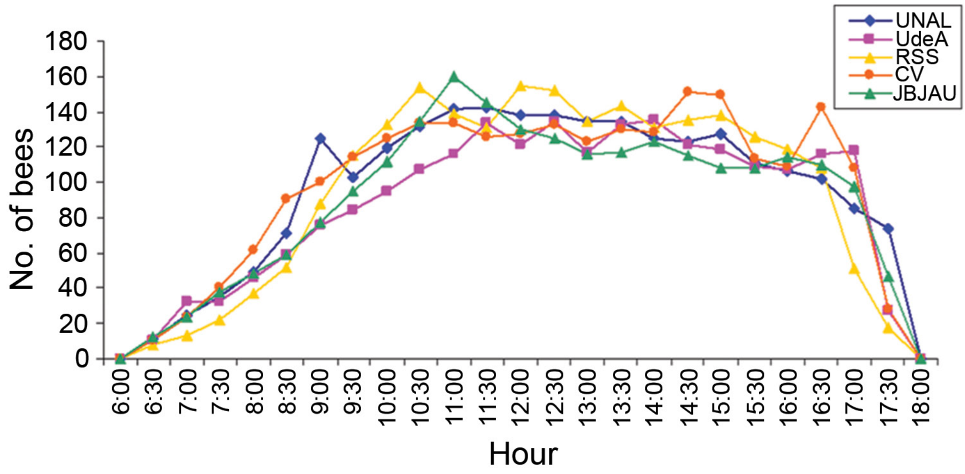

Figure 3. Daily foraging activity of *Tetragonisca angustula* (Latreille) in a forested area (Reserva San Sebastián [RSS]) near the city of Medellín, Colombia, and at four study sites within Medellín: Universidad Nacional (UNAL), Universidad de Antioquia (UdeA), Cerro el Volador (CV), and Jardín Botánico 'Joaquín Antonio Uribe' (JBJAU).

RESULTS

Most nests of *T. angustula* in Medellín were found in cavities inside building walls (73%); remaining nests were located within cement posts and tree trunks. Nests were found at heights ranging from 0 to 250 cm ($\bar{x}$ = 38.8 cm, ± 55, n = 59) above ground and were often exposed to sunlight, although the degree of exposure varied among sites and among nests (Table 1). The entrance tube had an average length of 5.2 cm (± 5.6, n = 59) and 1.0 cm (± 0.2, n = 59) in diameter. About 7–11 workers were observed hovering in front of the nest entrance at any given time ($\bar{x}$ = 9.7, ± 2.4, n = 59), and no significant differences (p = 0.0518) were noted before and after colored rings were added around the tube.

In Medellín, *T. angustula* started foraging at sunrise, as early as 6:00 hours. In all localities within the city, a progressive increment in the number of foragers was observed between 6:00 and 11:00 hours, decreasing from about 15:00 hours to 18:00 hours (Fig. 3). A multiple linear regression analysis between the ambient temperature, relative humidity, and light intensity showed a significant effect on the number of foraging bees (p = 0.0000; n = 18 nests; 260 minutes of observation per nest). About 45.3% of the variation on the number of foraging bees can be explained by variation in these three environmental variables. However, a linear regression analysis for each environmental variable showed that only light intensity (p = 0.0003) and ambient temperature (p = 0.0001) directly affected the number of foraging bees. Relative humidity did not seem to affect the number of foraging bees (p = 0.7896).

We did not find significant differences (p = 0.9104) between the average number of bees per interval of five minutes entering the nest in the city when compared with that of the forested area. Thus, the higher ambient temperature and light intensity in Medellín do not significantly affect the daily foraging activity of *T. angustula*.

During the eight months that nests were followed, only six of the 59 nests (~10%) disappeared. Five of these nests were marked (three with red, two with black). Marked nests were often disturbed by people as marks were sometimes removed, and the entrance tube removed or plugged with garbage, pebbles, and sticks. The nest entrance of one nest was covered with cement. Similar evidence of disturbance was observed in the remaining seven marked nests. Because we did not follow all nests every day, we do not know the frequency of disturbance on these nests. Some nests may have been disturbed multiple times as bees removed the debris and rebuilt a new entrance tube.

Both female and male geckos [*Gonatodes albogularis* (Duméril & Bibron) (Squamata: Gekkota: Sphaerodactylidae)] were observed on several occasions hunting bees in front of marked as well as unmarked nests. No other predators were observed.

DISCUSSION

Our observations on the daily foraging pattern of *T. angustula* in Medellín agree with previous reports (*e.g.*, de Bruijn & Sommeijer, 1997) and indicate that it does not significantly differ between urban and forested environments. Perhaps the pale body coloration and small size of *T. angustula* may facilitate foraging under these open, warmer, urban conditions, as these two features have been shown to have a significant effect on body thermoregulation. Light-colored bees tend to warm up less rapidly than dark-colored bees. Also, small bees tend to gain and lose heat more rapidly, although they will not attain excessively high body temperatures because convective heat loss is proportional to surface area (Pereboom & Biesmeijer, 2003). Further observations could be focused on detecting differences, if any, of the various foraging activities of the colony, such as nectar or pollen collection.

Our observations also indicate that nests of *T. angustula* are often largely undetected and undisturbed by people in Medellín. A few other species of stingless bees are also often found in lowland semi-urban and urban environments in Colombia, including Medellín, such as some species of *Nannotrigona* Cockerell, *Partamona*, *Scaptotrigona*, and *Trigona* Jurine. Except for *Nannotrigona*, these bees tend to be larger in body size and much more aggressive at defending their nests than *T. angustula*. Additionally, their nests are often exposed or partially exposed, usually large, conspicuous, and made of mud (*e.g.*, Wille & Michener, 1973; Michener, 1974). Their honey is also rarely exploited. Even though those species are potentially able to survive in urban environments, their nests tend to be removed either because they may become a nuisance due to their aggressive behavior or are not aesthetically pleasant (V.H. Gonzalez, pers. obs.). This is not the case for *T. angustula*, which is more docile and has more inconspicuous nests.

The low proportion of destroyed nests of *T. angustula* in Medellín suggests that nest mortality might be very low, as observed by Slaa (2006) in Costa Rica. This author estimated that the colony life span for *T. angustula* in deforested areas (not urban areas) is about 12.5 years, three times longer than in the forest. The possibility that some nests in Medellín could have been replaced by a queen or colony without being detected during our monthly surveys cannot be ruled out. If that is the case, mortality could have been slightly higher than that observed.

Several features of the biology of *T. angustula* may account for its success in urbanized areas, which includes: 1) high reproduction rate and relatively fast swarming process after a suitable cavity is found (Slaa, 2006); 2) small colony size and wide range of nest sites and substrates that facilitate the occupation of any small cavity anywhere (*e.g.*, Schwarz, 1948; Vergara *et al.*, 1986; Nates-Parra, 2005); 3) small body size and pale body coloration that allow them to forage under conditions with higher ambient temperature and sunlight (Pereboom & Biesmeijer, 2003); 4) highly polylectic diet (*e.g.*, Almeida *et al.*, 2012) that facilitates access to a wide variety of plants, including exotics; and 5) unflashy, largely hidden nests as well as a nonaggressive defensive behavior against large vertebrate intruders, which increases concealment. The latter characteristic also might reduce the chances that the nests are removed by people in the city.

The synanthropic behavior of *T. angustula* offers a unique opportunity to address interesting biological and ecological questions. For example, how do socionomic variables affect the density of nests in the city? In Colombia, low income neighborhoods are usually depauperate of green areas (street gardens, parks, *&c.*) and a lower nest density might be expected. What are the pollen diet and foraging strategies of *T. angustula* in urban environments? Is their specialized guarding behavior, which is composed of two set of guards, modified in response to the absence of attacks by *Lestrimelitta* in the city? What is the population structure and genetic composition of *T. angustula* in urban environments? Understanding these aspects of the urban ecology of *T. angustula* could also be useful when designing projects to promote meliponiculture in urban and semi-urban settings.

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