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EDITED BY
Helen Wallace,
Queensland University of Technology, Australia

REVIEWED BY
Taimy Cantillo,
State University of Feira de Santana, Brazil

*CORRESPONDENCE
Isabel Alves-dos-Santos
isabelha@usp.br

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Knowledge gaps on Neotropical solitary bees

Isabel Alves-dos-Santos[1]* and Maria Cristina Gaglianone[2]

[1]Ecology Department, Instituto de Biociências, Universidade de São Paulo - USP, São Paulo, SP, Brazil, [2]Environmental Sciences Laboratory, Universidade Estadual do Norte Fluminense Darcy Ribeiro - UENF, Campos dos Goytacazes, RJ, Brazil

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Introduction

Solitary bees represent the vast majority of Apiformes species (Michener, 2007). With the exception of the subfamily Nomadinae (which are cleptoparasitic bees), the solitary lifestyle is present in all other Apiformes subfamilies, totaling approximately 15,500 species (Danforth et al., 2019). This represents approximately 77% of bee diversity. In solitary bees, there is no cooperation or intergenerational contact (Michener, 1974). The female builds the nest alone, provisioning and defending it (Batra, 1984; Alves dos Santos, 2002, Neff, 2008). In each cell built, the female lays an egg. After hatching, the larva passes through four or five stages, consuming the food supplied by the mother before pupating. The adult then emerges and restarts the species cycle. These phases can last a few weeks or many months. In any case, offspring and mothers never meet.

Some solitary bees build nests in pre-existing cavities, such as holes left by beetles in wood-rotting tree trunks or various hollow branches. In this case, nests of these species can be obtained by offering artificial traps, such as bamboo segments or perforated wood (Krombein, 1967; Garófalo et al., 2004). This technique greatly facilitates the collection of data on the biology of the species (Alves dos Santos, 2002) and enables their use on a larger scale for commercial purposes (e.g., *Osmia cornuta* and *Megachile rotundata*, both used for crop pollination) (Stephen, 1961; Richards, 1984; Bosch and Kemp, 2002; Muniz et al., 2024).

However, the vast majority of solitary bee species (three-quarters) nest in the ground, excavating their own nests (Danforth et al., 2019; Antoine and Forrest, 2021). In this case, to study them, the first challenge is to find the nest, which is often just a small hole in the ground. Many species form aggregations, which are several nests in proximity, and when the species is active, there is strong movement in the area, signaling the presence of nests (Cane, 2024). In some species, these aggregations are permanent, meaning they become active annually and can increase significantly in size (Batra, 1999; Cane, 2003).

After finding a solitary bee nest on the ground, the second challenge is excavating it to reach the brood cells. Luckily, the nests are shallow (Celary, 2004) or have few branches, making them easy to excavate. However, several species have deep nests in hard or sandy soil, requiring time-consuming and careful excavation (Bohart et al., 1972; Roberts, 1973; Gaglianone, 2000). These two steps make it difficult to obtain data on the biology of most solitary species. Access to the nest provides a unique opportunity to obtain data on the plants on which the species depends entirely, the potential enemies, seasonality of the species, offspring development, nest architecture, and more.

To illustrate the current knowledge gaps regarding solitary bees, we draw on data from two important groups of the Neotropical apifauna: the Eucerini tribe, which is well represented on all continents except Australia, and the subfamily Diphaglossinae, which is restricted to the Americas. These groups are commonly recorded in surveys of Neotropical bee fauna, although usually at low abundances, which further hampers the understanding of their biology. In this review, we examined the literature published over the past 10 decades addressing the biology of these bees as indexed in the Web of Science database.

Knowledge of the biology of Neotropical Eucerini

The tribe Eucerini comprises 780 species (Michener, 2007), with some very speciose genera, such as *Eucera*, from the Northern Hemisphere. Eucerine bees show particularly high genetic diversity in the Western Hemisphere (Dorchin et al., 2018), with 31 genera, 16 subgenera, and 247 species (Urban et al., 2023), occurring from Quebec, Canada, to Chubut, Argentina. Representatives of this tribe are popularly known as long-horned bees, as the males have extremely long antennae (Figure 1), sometimes twice the size of females. There are reports of male roosting in flowers or branches, in aggregates of several species (Alcock, 1998; Mahlmann et al., 2014; Silva and Andrade, 2022).

All Eucerini species nest on the ground. A compilation of research published over the last 100 years on nesting in Eucerini revealed that only approximately 4% of the species have been studied (32 species) (Table 1). The studies describe the nests, the number and arrangement of brood cells, and in many cases, also provide data on the immatures, associated parasites, and plants used. However, even among the 32 species studied, there are gaps in some of this information. Some of the most complete studies in terms of description about the species are those by Rozen (1964) on *Svastra obliqua* in Florida; by Parker et al. (1981) on *Melissodes agilis* in Utah, USA; and by Michelette et al. (2000) on *Canephorula apiformis* in San Juan, Argentina.

Common to most Eucerini are the oval-shaped cells, vertically oriented, with a thin cell lining, eggs placed on top of the provision, pollen packed into the base of cells, liquid layer covering pollen masses. The mature larva places its feces against the cell cap and then spins a thin cocoon, constructed of a number of coarse and fine layers of silk. Rozen (1991) compared the anatomical structures of the mature larvae of the Eucerini. Several species are polylectic, such as *Eucera hamata* (Miliczky, 1985) and *Thygater aethiops* (Gonzalez and Ospina, 2008), and others are oligolectic, such as the pumpkin specialist *Peponapis* and *Xenoglossa* (Hurd et al., 1971). Nests of three *Peponapis* species have been described. They form small nesting aggregations (six to eight nests) adjacent to *Cucurbita* fields, which they pollinate (Hurd et al., 1971). Usually, the brood cells reveal 100% pollen from *Cucurbita* (Krug et al., 2010).

Of the 32 Eucerini species studied, 14 occur in the Neotropics, but there are numerous hiatuses. For example, there are no nest studies on the genus *Florilegus* (11 species) or *Gaesischia* (31 species), only one study on *Alloscirtetica* (44 species), and two studies on *Melissoptila* (54 species). Thus, even for the most common and specious genera in the Americas, we have no information on their biology, as their nests have never been located. The Brazilian Eucerini species are well-resolved systematically due to the dedication of Danúncia Urban with this tribe (Urban et al., 2023). Several species are oligolectic, such as *Florilegus* (specialist on *Pontederia*) or *Gaesischia* (specialist on *Vernonia*) (Schlindwein, 1998). However, their nests remain undetected and may require more intensive and careful field efforts to be found.

FIGURE 1
Males of the groups discussed in the text: *Trichocerapis mirabilis* (note the typical long antennae) and *Ptiloglossa pretiosa* on flower of Lamanonia ternata (Cunoniaceae). Photos credit: Adriana Tiba and Julio Pupim.

TABLE 1 Studies on nesting biology of Neotropical solitary bee's species of the tribe Eucerini and subfamily Diphaglossinae.

Bee group / Species	Nest	Associated plants*	Parasites	Immatures	Locality	References
Apidae Eucerini						
Alloscirtetica gayi; A. tristigata	(?)	Asteraceae (?)	🔍	☑	Chile	Claude-Joseph, 1926 (apud Rozen, 1991)
Canephorula apiformis	☑	Polylectic; *Atamisquea emarginata*, *Tessaria*	*Melectoides bellus*	☑	San Juan, Argentina	Michelette et al., 2000
Melissodes floris	☑	🔍	🔍	🔍	Guatemala	Batra and Schuster, 1977
Melissodes nigroaenea	☑	*Cosmos*	🔍	🔍	Paraná, Brazil	Michener and Lange, 1958
Melissodes persimilis	☑	Asteraceae	🔍	☑	Puntarenas, Costa Rica	Buchmann and Jones 1980
Melissoptila paraguayensis	☑	🔍	🔍	🔍	S. J. Pinhais, Brazil	Michener and Lange, 1958
Melissoptila pubescens	☑	🔍	🔍	🔍	Tigre, Argentina	Moffatt and Roig Alsina 1992
Peponapis crassidentata	☑	*Cucurbita*	🔍	🔍	Mexico	Delgado-Carrillo et al., 2017
Peponapis fervens	☑	*Cucurbita*	🔍	☑	Paraná, Brazil	Michener and Lange, 1958; Krug et al., 2010
Peponapis utahensis	☑	*Cucurbita*	🔍	☑	Jalisco, Mexico	Rozen and Ayala 1987
Thygater analis	☑	*Cassia*	🔍	☑	Curitiba, Brazil	Michener and Lange, 1958; Rozen 1974
Thygater aethiops	☑	Polylectic	fly	🔍	Colombia, altiplano	Gonzalez and Ospina, 2008
Xenoglossa fulva	☑	*Cucurbita*	🔍	☑	Guanajuato, Mexico	Linsley et al., 1955
Colletidae Diphaglossinae						
Cadeguala albopilosa (Policana albopilosa)	☑	🔍	🔍	☑	Chubut, Argentina; Palena, Chile	Claude-Joseph (1926); Sarzetti et al., 2013
Cadeguala occidentalis	☑	🔍	🔍	☑	Viña del Mar, Chile	Torchio and Burwell 1987; Montalva et al., 2011
Caupolicana gayi	☑	🔍	*Doeringiella*	🔍	Chile	Rozen, 1984
Crawfordapis luctuosa	☑	Polyletic	Meloidae	🔍	Costa Rica, Panama	Otis et al., 1983; Roubik and Michener, 1985; Wuellner and Jang, 1996
Diphaglossa gayi	☑	🔍	🔍	☑	Palena, Chile	Sarzetti et al., 2013
Ptiloglossa fulvopilosa	☑	🔍	*Odyneropsis*	☑	Trinidad	Rozen, 1984
Ptiloglossa guinnae	☑	Melastomataceae	*Odyneropsis* mites	🔍	Costa Rica	Roberts, 1971
Ptiloglossa latecalcarata	☑	*Caryocar;* Myrtaceae	🔍	🔍	S. G. Rio Preto, Brazil	Araujo et al., 2020
Ptiloglossa matutina	☑	🔍	🔍	☑	Misiones, Argentina	Sarzetti et al., 2013
Ptiloglossa tarsata	☑	*Solanum*	🔍	☑	Salta, Argentina	Sarzetti et al., 2013
Zikanapis tucumana	☑	*Solanum*	🔍	☑	La Rioja, Argentina	Sarzetti et al., 2013

Symbols: ☑ = data available; 🔍 = data missing; (?) = unsure data. *Refers to the pollen sources the species uses to feed its immatures.

Knowledge of the biology of Diphaglossinae

The subfamily Diphaglossinae is composed of large bees of the Colletidae family, restricted to the New World (Michener, 2007). The subfamily is divided into three tribes, 12 genera, and approximately 130 species (Danforth et al., 2019). Like the Eucerini, all Diphaglossinae species are solitary and nest on the ground. The species are notable for their beautiful colors and abundant hairiness (Figure 1). A common characteristic of most species in this subfamily is their crepuscular habit, which makes locating their nests in the wild even more difficult, as the nest is closed all day. Females are active for only a brief window of time at twilight (Danforth et al., 2019).

Investigations on the nesting biology of Diphaglossine bees correspond to studies on 14 species, approximately 10% of their representatives (Table 1). Of these 14 studies, 11 were conducted on Neotropical species and the other 3 in Arizona (Linsley and Cazier, 1970; Rozen, 1984). In South America, the study conducted in Argentina and Chile with five species is noteworthy (Sarzetti et al., 2013). Recurrent parasites belong to the genera *Triepeolus* and *Odyneropsis*, both of the tribe Nomadini.

Common to the studied species is the nest with a deep vertical tunnel, with lateral branches radiating from the main burrow in various directions, each ending in a single cell. The branches are filled with soil after oviposition. The brood cells are large to very large (corresponding to the large size of the bees), elongated, with a diameter somewhat larger than the diameter of the burrow, and circular in cross section. The brood cells are vertically oriented and curved at the top, which can reach 90° or more (*Ptiloglossa* and *Crawfordapis*) (Rozen, 1984; Sarzetti et al., 2013). The cells are lined with a cellophane-like layer and contain semiliquid provisions. For some species, huge and permanent aggregations have been reported (Roberts, 1971; Otis et al., 1983; Roubik and Michener, 1985).

A recent study of *Ptiloglossa latecalcarata* conducted in the Brazilian cerrado revealed a curious fact: the presence of monofloral pollen in the brood cells. In this case, the recorded pollen was of *Caryocar brasiliense* (Caryocaraceae), known as pequi, described as a chiropterophilous plant, and visited by nocturnal bees at twilight (Araujo et al., 2020). The flowers of this species open in the evening and provide resources until dawn, supplying a significant amount of pollen for nocturnal bees. However, it is known that *P. latecalcarata* is not a specialist on *Caryocar* but rather and opportunist for the plant with nocturnal anthesis and massing flowering around the nest. A similar behavior was observed on *Campomonesia phaea* (Myrtaceae) (Cordeiro et al., 2017). The females have a short window of time to forage and collect pollen and nectar for the offspring provision. Thus, the plant that is nearby can be the target pollen source.

Discussion

Using these two groups of Apiformes, Eucerini and Diphaglossinae, we tried to illustrate the gaps of knowledge on solitary bees in the Neotropics. However, we believe that similar limitations exist in other biogeographical regions in the world. We attribute these gaps to many factors, but we highlight one less discussed: descriptive or natural history papers are "out of fashion" and are not seen as high-impact results by journals or modern researchers. We disagree with this trend, as basic data on the biology of any species fuel discussions of "advanced papers" addressing evolutionary questions, phylogenetic relationships, population genetics, and species interaction networks, among others. Classic studies of the biology of species can yield extensive insights into the group (Gaglianone, 2005). The following two examples illustrate how such studies provide valuable information.

With accumulated information on the immatures of many cleptoparasitic species and observations of the strategies of females in nests of all the tribes in the Neotropics, Rozen (2003) contributed substantially to the understanding of the evolution and phylogenetic relationships within the extensive cleptoparasitic subfamily, Nomadinae, the oldest clade of parasitic bees (Sless et al., 2021). Gathering such information was only possible through meticulous nest excavation and description of the larval anatomy of different lineages of cleptoparasitic bees, primarily from Neotropical regions, over many years.

Through access to the nest of the European *Andrena marginata*, Stenmark (2013) was able to obtain a huge amount of data on foraging behavior, pollen provision, pollen utilization, development, sex ratio, and nest architecture in Sweden. However, the substantial highlight was that with his results, he was able to estimate the critical pollen resources needed for a nest and for an entire bee population, that is, predicting the carrying capacity (*K*-value) of bee populations in the habitat. Thus, he proposed a model with easily measured variables (the plants available in the area) that can be used as a tool in bee conservation planning. These two cases demonstrate the importance of information on species' biology obtained through field observation and experimentation.

Bees, like all insects, face numerous threats. The fact that they have been less studied already poses a risk to solitary bees (Alves dos Santos et al., 2025). We cannot protect organisms if we do not know where they live and what they depend on. In Europe, the list of endangered species includes approximately 60% of bee species with insufficient data (Nieto et al., 2014). This deficiency prevents a conclusive assessment of the species' conservation status. For the Neotropical region, this percentage is certainly much higher.

In conclusion, it would be very important for basic natural history studies to be given greater prestige by journals and the scientific community, taking into account the contribution they can make in several cutting-edge areas. Thus, we encourage young scientists to leave the comfort of air conditioning and venture into fieldwork, where things happen. Soga and Gaston (2025) mention several negative impacts on science and education associated with the reduction in fieldwork experience. Furthermore, observing the activity of females building nests is very pedagogic, as well as very enjoyable. With a good protocol and some instruments, a wealth of data can be achieved.

Author contributions

IA: Conceptualization, Investigation, Validation, Writing – original draft, Writing – review & editing. MG: Conceptualization, Validation, Writing – review & editing.

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In memoriam

We dedicate this paper to our dear colleague, Fernando do Amaral Silveira, a great bee systematist, who died prematurely, leaving a gap among bee researchers in Brazil.

Conflict of interest

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