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Mating System and Sleeping Behaviour of the Male and Female *Centris* (*Paracentris*) *burgdorfi* Friese (Apidae, Centridini)

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Abstract We describe the mating behaviour of males of *Centris* (*Paracentris*) *burgdorfi*, a solitary, univoltine bee, with a wide distribution in Brazil. We also describe the unusual sleeping sites of males and females. The study was performed during two breeding seasons, in northeastern Brazil, where the species nests in aggregations in petrified dunes. Data on mating behaviour were collected through direct observations of the bees at the nesting-emergence site. Males compete intensely for virgin females in the morning, sometimes killing rivals. The high competition for females near the nesting site makes that the male has to take the female to another place to get genital contact. In the evening, males do not use plants to spend the night, instead they aggregate in sleeping clusters inside old burrows in the nesting-emergence area while females sleep in groups on plants that provide the floral oil used in nest construction.

Keywords Mating behaviour · oil-collecting bee · sexual selection · sleeping aggregation · solitary bee

Introduction

Animal mating systems focus on the tactics used by individuals in sexually reproducing species (Kokko et al. 2014). Studies on mating systems have involved vertebrate (e.g., Orians 1969; Foltz 1981; Fleischer 1996; Mabry et al. 2013) and invertebrate animals

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(e.g., Bateman 1948; Miller and Tsao 1974; Eberhard 1991; Muniz and Machado 2015). The mating tactics of solitary bees, have also been described. In most cases, male solitary bees are easily observed, given their active behaviour and constant search for receptive female solitary bees (Paxton 2005). Male bees may search for virgin female bees in the emergence-nesting area (e.g., Hiller and Wittmann 1994; Ayasse et al. 2001), or they may patrol the flowering plants usually visited by resource-collecting females (e.g., Alves-dos-Santos 1999; Alcock et al. 2010). In addition, males of the same species may utilize alternative tactics, as in cases where large males fight for emerging females, whereas smaller males exhibit less aggressive tactics patrolling plants without any aggressiveness with other males (Alcock et al. 1977; Danforth 1991; Paxton 2005; Oliveira and Schlindwein 2010). Territorial males can also protect an emergence site or a particular group of plants and dig nests searching for females while males intruders try to take his place (e.g. Alcock et al. 1976). The evolution of alternative mating tactics is directly related to variation in the ability of males to secure access to receptive females (Alcock 2013).

Male bees are under selection to maximize their individual reproductive success in an environment in which receptive female bees are a limiting resource (Alcock et al. 1978), sometimes resulting in fighting among the males for mates. The intensity of sexual selection in male bees is generally related to the degree of rarity of female bees (Shuster 2009). Single mating by the females, which is a common behaviour for most solitary bees (Paxton 2005), promotes competition, since the number of sexually receptive females is lower than the number of sexually active males. The greater the number of mature males in relation to the number of receptive females, the higher the Operational Sex Ratio (OSR) and the stronger the competition among males (Ahnesjö et al. 2001). Generally, males emerge a few days before the females and rapidly start the search for receptive virgin females (Alves-dos-Santos 1999). This protandry means that even if the sex ratio is 1: 1, according to Fisher (1958), the number of males capable of mating is much higher than the number of females, thereby generating strong competition among males.

The hypothesis about the association between the spatiotemporal distribution of receptive females and the males' behaviour predicts that if the females nest aggregated the males will searching for receptive females at nest sites (Alcock et al. 1978; Ayasse et al. 2001; Paxton 2005). In dispersed nests, like bees that use pre-existing cavities, would become more difficult to find females, being more likely males searching for females in the flowers. Also, the high density of males would lead to a high competition between them while low density would stimulate the territoriality (Alcock et al. 1978; Ayasse et al. 2001; Paxton 2005).

The genus *Centris* Fabricius includes about 230 species of solitary bees found from Argentina to the southern United States (Moure et al. 2007). Identification can be difficult due to the complex taxonomy of the group (Vivallo and Zanella 2012). Many species of *Centris* collect floral oil, a resource used in feeding the larvae and in forming the cell lining (Vogel 1990). Although they are mostly abundant in the humid tropical areas, some species are found in semi-arid regions. The subgenus *Centris* (*Paracentris*) Cameron, for example, is most commonly represented in semi-desert Andean regions or in the semi-arid region of northeastern Brazil (Zanella 2002). Among the species found in this subgenus, *Centris* (*Paracentris*) *burgdorfi* Friese is a univoltine, protandric species, makes nest aggregated, widely distributed in Brazil and also occurring in some parts of Argentina and Paraguay (Zanella 2002). Females of *Centris,* like other solitary bees, frequently nest close to one another and sleep in these nests, whilst males sleep in the field, grouped under plants (Michener 2007).

Studies on the behaviour of *Centris* males have been carried out on some species, including *C. crassipes* Smith, *C. dirrhoda* Moure and *C. fasciata* Smith (Raw 1975), *C. pallida* Fox (Alcock 1976; Alcock et al. 1976; Alcock et al. 1977), *C. adani* Cockerell (Frankie et al. 1980), *C. heithausi* Snelling (Coville et al. 1986), *C. lutea* Friese and *C. decolorata* Lepeletier (Raw 1975; Alves-dos-Santos et al. 2009, cited as *C. leprieuri*), although more studies have addressed the nesting behaviour of females (e.g., Rozen and Buchman 1990; Aguiar and Gaglianone 2003; Rego et al. 2006; Ramos et al. 2007; Martins et al. 2013).

Although *Centris* genus has many species, our comprehension concerning to males" reproductive tactics or localities where both males and females spend the night is something scarce. Hence, here we address three important questions 1) What mating tactics are employed by the males of this species? 2) What is the daily activity pattern of males? 3) Where do males and females spend the night? Based on hypothesis about the association between the spatiotemporal distribution of receptive females and about male density we predict a high competition for females at nest sites.

Material and Methods

Study Site

Data on mating and sleeping behaviour of *C. burgdorfi* were collected from a touristic region known as "Deserto dos Anjos" (05° 36′ S, 35° 14′ W; altitude: 41 m), near the city of Natal, in Rio Grande do Norte state in northeastern Brazil. The region is located in a transition zone between areas that are hot and humid, due to high rainfall, and areas that are hot, but semi-arid due to strong evaporation (Nogueira 1982). The average annual temperature is 26.7 °C, with little variation throughout the year. The rainy season covers the period from March to August, with average annual rainfall of about 1640 mm (INMET/UFRN 2002).

Centris burgdorfi nests in geological formations, known as petrified dunes (Silva et al. 2012). These petrified dunes can form walls up to 50 m in height (Neto et al. 2005). These formations were produced at the edge of the sea when the current coastal plain was formed (Meireles and Santos 2012).

During the flight season of the bee, between April and July, the sun rises at 05:15 a.m. and sets at 05:30 p.m. Data on the behaviour of *C. burgdorfi* males were collected daily, between 04:30 a.m. and 05:30 p.m., in two breeding seasons, between April and May, 2014 (247 h of observation in 19 days) and between May and June, 2015 (208 h of observation in 16 days).

Tactics for Finding Receptive Females

In order to quantify the activity of the males, we counted for 12 days the number of males seen flying in the emergence-nesting area. The males were marked over thorax in the sleeping aggregation with different combinations of colours with a non-toxic paint pen (Posca® - Tokyo, Japan) in order to avoid count the same individual more than once.

When there were fewer males at the site (about 30 individuals), males flew near the nest entrances with little interaction, allowing an accurate count of individuals. With increasing number of males, the bees constantly chased one another and so was difficult an accurate count. By the fact that the males fly uniformly on the aggregation was possible estimate the number of males flying. Using a fixed location in front of the aggregation, we count the number of males flying in a given area and estimate the number of males present in the rest of the nesting area. Even though this number does not represent the actual number of males present, it gives us an estimate of the total value at a particular time of day. The counting of the males was made every half an hour, covering the period just before the activity start to the time they were not observed in the aggregation. Using this methodology, it was possible to estimate the period when the activity of males searching for females was highest. The temperature was measured in front of the nesting site with a standardized digital thermo-hygrometer. We tested for an association between male activity and the temperature using a Spearman "two sided" rank-correlation test. Statistical analyses were made using Statistica 10.0.

Male and Female Behaviour at Plants

The species of plants used by the males and females were recorded, based on observations of the bees on the flowers and an analysis of the pollen collected from bee bodies or from bee nests (Sabino et al. in prep.). Using these methods, it was possible to know which plants males and females were visiting in the field being possible to monitor the behaviour of males in the plants.

Mating Behaviour

Copulations were videotaped and the behaviour of the males and females was recorded, as well as the time of copulation. The videos were later analysed to help describe the mating behaviour in a detailed fashion. To check for loss of attractiveness of mated females, a total of 20 females were marked on the thorax after the emergence and were observed throughout the nesting season.

Sleeping Aggregations

After finding groups of sleeping males and females, we marked individually bees at these locations with paint dots on the thorax to assess the fidelity of the bees to their sleeping sites. We count the number of individuals present in the place that they use as a dormitory. The numbers are presented by mean ± standard error.

Results

Searching for Receptive Females

Males searched for emerging females in the areas where females had nested in the previous year and only in the morning of sunny days. On rainy days, few males were seen searching inasmuch as most males looked for shelter in the same galleries of petrified dunes that they used as a dormitory. The period of highest activity of males was between 09:00 a.m. and 10:30 a.m. Male patrolling activity subsequently declined sharply and ended at noon. Despite the increasing in temperature throughout the morning (which reached a maximum of about 36 °C at 12:00 p.m. (Fig. 1)) there is no correlation between male activity and temperature (rs = 0.19; $p = 0.48$).

When relatively few males were present, individual bees attempted to control access to emergence holes by flying from one side of the tunnel entrance to the other, so as to prevent other males from stationing themselves around places from which emerging virgin females might appear. Territorial males sometimes collided with intruders or chased them some distance away. Occasionally, a territorial male and intruder might fall to the ground together. These fights sometimes ended in the death of one of the combatants by bites ($n = 3$).

At times, when males were not chasing or fighting with intruders, they covered the nest entrance with their legs, so as to control access to emerging females. Males stationed at emergence holes often lifted a leg and exposed the tibial spur to another male that had approached the spot (Fig. 2).

On three occasions, we observed males digging into the petrified sand dune down to a cell that contained a virgin female and fighting for the spot with other males. On other occasions, the males were seen entering the emergence tunnels and subsequently mounting a female, with the pair flying off to copulate elsewhere ($n = 2$).

Behaviour at Plants

Males and females were observed collecting nectar on flowers of *Stilpnopappus cearenses* Huber (Asteraceae), *Centrosema* sp. (Fabaceae), and especially on flowers of *Cuphea* sp. (Lythraceae). We observed males ($n = 5$) patrolling on *Cuphea* sp. flowers, searching for females. Each male had a small territory, which comprised only one plant. The males sometimes tried to control access to a small patch of flowers, chasing off competitors until only one male held the territory. The males' strategy in searching for females was compiled together with literature data about others *Centris* species (Table 1).

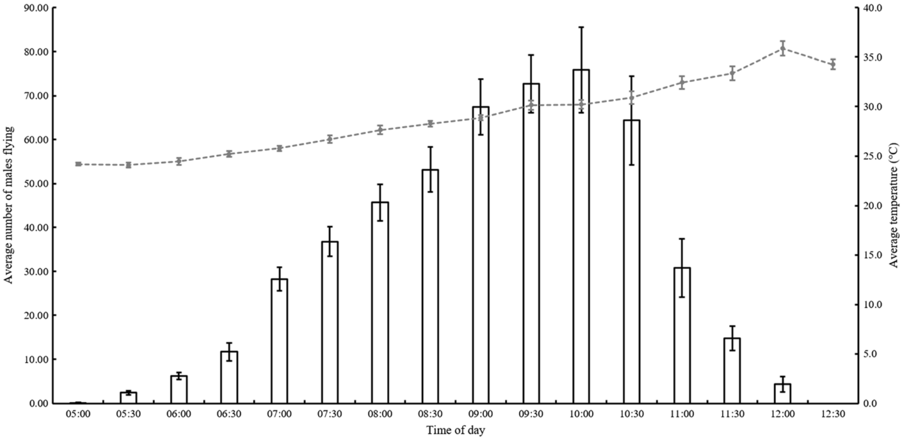

Fig. 1 Variation in the daily activity of *Centris* (*Paracentris*) *burgdorfi* males on patrol in the nesting area. The bars represent the average of males throughout twelve days with their standard errors. The dashed line represents the average temperature measured during the same period with standard errors

Fig. 2 *Centris* (*Paracentris*) *burgdorfi* male defending a tunnel in a petrified dune that was both a nest entrance and the potential exit for emerging virgin females. Notice that the perched male is using his left foreleg and midleg to ward off the intruder

Mating Behaviour

When the female emerges, males crowd around her (Fig. 3a), but most do not achieve genital contact. Instead one male grasps the female and flies away with her, far from the other males. When the pair alight, as far as 200 m or more from the spot where the female emerged, copulation is completed in 6.99 ± 0.31 min; (mean ± SE; $n = 11$). During copulation, the male uses his front legs to immobilize the female and to support the pair on the substrate, while the middle legs prop up the midlegs of the female, so that she cannot support herself on the substrate. With his hind legs, the male immobilizes the female's wings and attempts to lift her abdomen in order to promote coupling. After genital coupling occurs, the male vibrates his wings continuously, producing a buzzing sound, while at the same time touching the female antennae repeatedly (Fig. 3b). During copulation, the male frequently interrupts genital contact in order to rub a hind leg against the female's abdomen.

Copulation may occur entirely in one place, usually a hard, flat surface. In situations where mating occurs on soft substrates, such as branches of plants or flowers, the male often carries the female to several locations, holding her body with his front and middle legs, while flying about 50 cm from the ground. Whenever the pair alight, the male attempts to make genital contact as the female holds onto the substrate (Fig. 3c). The female appears to contribute to flight by flapping her wings.

After mating the female remains still for a few seconds before beginning a series of abdominal contractions, after which she rubs the inner part of her hind legs on her abdomen (Fig. 3d). Immediately after mating, the females become unattractive, such that even when other males approach mated females, they do not try to copulate. None of the females marked after mating and observed while nesting were ever seen copulating again. After copulation is completed, males return to the emergence area and compete again with other males for new females.

Table 1 *Centris* species classified according nest density and male behaviour

Centris species	Female (nest) density	Male behaviour	References
C. (*Centris*) *adani*	Dispersed	Territoriality in food plants	Frankie et al. 1980
C. (*Centris*) *decolorata*	Aggregated	Territoriality in the nesting site	Raw 1975; Alves-dos-Santos et al. 2009
C. (*Centris*) *dirrhoda*	Aggregated	Territoriality by landmarks	Raw 1975
C. (*Centris*) *fasciata*	Dispersed	Territoriality in food plants	Raw 1975
C. (*Hemisiella*) *crassipes*	Dispersed	Territoriality by landmarks	Raw 1975
C. (*Paracentris*) *burgdorfi*	Aggregated	Scramble competition in the nesting site and territoriality in food plants	This work
C. (*Paracentris*) *pallida*	Aggregated	Scramble competition in the nesting site and territoriality in food plants	Alcock 1976; Alcock et al. 1976; Alcock et al. 1977
C. (*Trachina*) *heithausi*	Aggregated	Territoriality in food plants	Coville et al. 1986

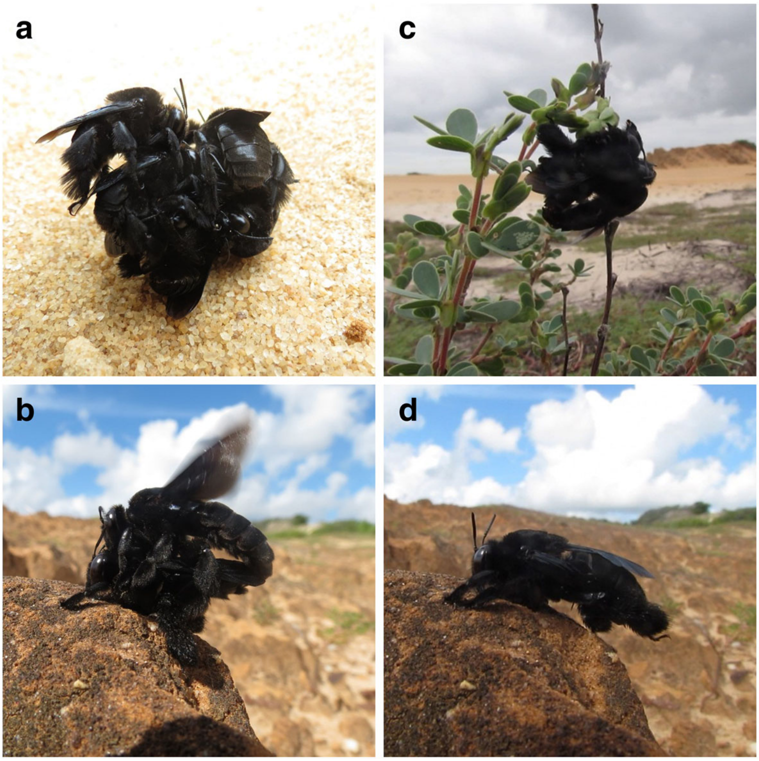

Fig. 3 Mating behaviour of *Centris* (*Paracentris*) *burgdorfi*. (**a**) Group of males around a female on the ground below the nest. (**b**) Male making genital contact with a female while vibrating his wings. (**c**) Mating on a plant branch in which the male is mounted on a female while the female holds the substrate. (**d**) Female beginning to use the inner part of her hindlegs to rub her abdomen shortly after mating

Unusual Sleeping Aggregations

Males spend the night in the vicinity of the nesting-emergence site, which they approach around 4:30 p.m. The resting place is at the highest part of the petrified dunes, which the first rays of sun reach at dawn. The first males to arrive occupy the various natural cavities, but are joined by other males to form groups in these places. Males that have been defending emergence tunnels arrive later, at around 05:30 p.m. We do not have the precise number of males inside de natural cavities, but the number of males outside was about 59.5 ± 1.02 ($n = 11$ days; Fig. 4).

The female bees do not spend the night in the same locations as the males. Instead, they aggregate in flowers and fruits of *Krameria tomentosa* A. St. Hill (Krameriaceae) (Fig. 5a). The dormitory of the females is located approximately 160 m away from the nesting site. All females were marked for two successive nights (42 females in the first night and 34 in second), with different colours, and this technique showed that females always returned to the same plant (Fig. 5b). By examining several other plants in the area, we found that females use *K. tomentosa* exclusively when sleeping (ca. 15 females per branch). By marking the females at night and observing them the next day, we learned that the plants are used both by females that were already building

Fig. 4 Sleeping aggregation of *Centris* (*Paracentris*) *burgdorfi* males at the top of petrified dunes

nests, and by females that were still seeking a nest site (Fig. 5c). The females arrive at their resting sites at around 05:00 p.m. and leave at 05:15 a.m.

Discussion

The Alternative Mating Tactics

Sexual selection has evidently resulted in males searching for females primarily during the period when potential matings are more likely to occur (Alcock 2013). Alves-dos-Santos (1999) observed a decrease in in male patrolling in five species of *Ancyloscelis* Latreille (*A. apiformis* Fabricius, *A. fiebrigi* Brèthes, *A. gigas* Friese, *A. turmalis* Vachal and *A. ursinus* Haliday) in the afternoon, which was associated with a possible decrease in the production and supply of nectar in plants and in the emergence of virgin females. Frankie et al. (1980) also associated reduced territory defence in *C. adani* males around 11:00 a.m. with the low amount of nectar available on the site.

Both males and females of *C. burgdorfi* visit the same flowering plants, as is true for many other solitary bees. For example, males of *Centris heithausi* Snelling visit the same flowering trees as females (Coville et al. 1986). Alves-dos-Santos (1999) found males of *Ancyloscelis apiformis A. fiebrigi*, *A. gigas*, *A. turmalis* and *A. ursinus* visiting the same flowers that females used as a source of nectar. This behaviour was also verified in *Centris scopipes* Friese, in which males and females collected nectar on *Memora pilgrim* (Miers) Sandwith (Bignoniaceae) (Gaglianone 2001). The male choice of the same flowering plants that the females uses indicates that, in addition to nectar source, males sometimes can mate with receptive females at flowers.

In solitary bees, the males of some species generally search for virgin females about to emerge from the last breeding season's nests (Hiller and Wittmann 1994; Mayer and Miliczky 1998; Ayasse et al. 2001). But some males of certain species may also patrol flowers where females forage preferentially (Villalobos and Shelly 1991; Alves-dos-Santos 1999; Alcock et al. 2010; Alcock and Buchmann 2011). The existence of alternative mating tactics suggests that not all females are immediately 'caught' by males as soon as they emerge (Alcock et al. 2010). As the activity of *C. burgdorfi* males

Fig. 5 Sleeping aggregation of *Centris* (*Paracentris*) *burgdorfi* females. (**a**) Group of females in branches of *Krameria tomentosa* at the end of the day. (**b**) Females marked on the late afternoon, as the sleeping aggregation forms. (**c**) A female marked at her sleeping site, returning to her nest in the morning

ceases late in the morning, females that emerge in the afternoon probably mate the next day, perhaps while foraging for nectar or pollen. Furthermore, some females may escape unmated from the emergence site while males are pursuing other females or males (Alcock 2013). In *Amegilla dawsoni* Rayment (Apidae) even though the high competition by males for females at the nesting site, some 10–20% of females leave the emergence site unmated (Simmons 2015). In many *Centris* species we observed males making territories even when the females nest aggregated (Table 1). These males mark territories by depositing a scent from their mandibular glands into the vegetation (Raw 1975). Males of *C. burgdorfi* showed a high competition for females at nest sites as predicted by hypothesis about the association between the spatiotemporal distribution of receptive females and male density. The same occur in *C. pallida* in Sonoran Desert, USA (Alcock 1976). But both species also exhibit different strategies in searching for females. The occurrence of different mating tactics of males within one species reflects the ability of individuals to adopt alternative behaviours, depending on the environmental conditions that they encounter (Alcock 1979).

The capacity of males to find pre-emergent females has been observed in some solitary bees (e.g., Alcock et al. 1976; Bergström and Tengö 1978). In *Centris pallida*, the digging males are common in the peak period of observed matings, suggesting that this behaviour has been biologically/or genetically programmed to coincide with the preferred time of emergence of the females (Alcock et al. 1976). Cane and Tengö (1981) demonstrated that components produced in the mandibular glands of receptive females of *Colletes cunicularis* Linnaeus (Colletidae) attract males, which find females in their brood cells even before they emerge. This ability enables males to mate with females before other competitors can (Alcock et al. 1976; Alcock 1980). If the same might be find in *C. burgdorfi*, then, this ability should be particularly advantageous for those males with higher chemical perception than theirs competitors since it is an aggregate nesting environment with intense competition, and single-mating females.

The Mating System of *Centris burgdorfi*

As copulation in *C. burgdorfi* is relatively long, it would be difficult to maintain full genital contact and also provide the hind leg stroking of the female in locations with many competing males. Due to the risk of interference during mating, it may be adaptive for males to copulate far from other bees, as has been suggested for *Centris pallida* by Alcock and Buchmann (1985). Alcock and Buchmann (2011) noted the difficulty in identifying the copulating male in *Habropoda pallida* Timberlake (Apidae), because of the great number of males clustering around a single recently emerged female. In *Epichars bicolor* Smith (Apidae), mating balls also formed around freshly emerged females even though only a single male actually copulated with a given female (Rocha-Filho et al. 2009). There was no full genital contact between males and females of *C. burgdorfi* during the time that males were competing with one another for females on the ground.

The significance of rubbing the female's abdomen in *C. burgdorfi* is unknown, although it could be a form of copulatory courtship that induces the female to release anti-attractant odours or it could be involved with the application of scents from the male that reduce the female's attractiveness. The change in the profile of the cuticular odour in post-mating females is known in solitary bees (Schiestl and Ayasse 2000; Paxton 2005; Simmons 2015) and this odour may even be transmitted to the female through the male, as recorded in *Osmia rufa* (Ayasse et al. 2001), *Centris adani* Cockerell (Frankie et al. 1980) and butterflies of the genus *Heliconius* Kluk (Gilbert 1976). The so-called 'anti-aphrodisiacs' is a method the male uses to ensure paternity in an extremely competitive environment (Ayasse et al. 2001). In solitary bees, it has been demonstrated that males are able to distinguish between the odours of receptive and non-receptive females (Frankie et al. 1980; Schiestl and Ayasse 2000). Chemical analyses are required to determine if the male of *C. burgdorfi* transmits some odour to the female or if he only induces the production of non-attractive compounds.

The pattern of wing movement, movement, antennal tapping, and the sound produced by males of *C. burgdorfi* occurred in all observed copulations. Copulatory courtship is very common in insects (Eberhard 1994) and a poor performance by a mating male may result in the rejection of his sperm by the female (Eberhard 1991). For example, males of the red flour beetle *Tribolium castaneum* Herbst rub the lateral edges of the females' elytra with their tarsi during copulation. In experiments realized by Edvardsson and Göran (2000) males without tarsi achieved a lower fertilization success than did males with unmanipulated legs. Vibrating signals seem to be common during the mating of solitary bees and wasps (Eickwort and Ginsberg 1980; Larsen et al.

1986). Vibrations are generated by rhythmic thoracic oscillations in the same manner that move the wings (Hrncir et al. 2006). In *Amegilla dawsoni* Simmons et al. (2000) also reported a similar sound produced by the male when interacting with the female during mating. *Osmia rufa* Linnaeus (Megachilidae) has a pre-mating behaviour and experiments have shown that the female has a preference for a male with a longer duration of pre-mating vibration, which can be indicative of his health and vigour (Conrad et al. 2010). There are also cases in which females produce sound (stridulate) to communicate to males the end of the copula, as in *Nemka viduata* (Mutillidae) (Tormos et al. 2010). According to the authors the stridulation of the female at the end of mating, as observed in *N. viduata*, possible could help the movement of sperm into the spermathecal. Nevertheless, in *C. burgdorfi* these movements also occurred between genital contact and we do not test the hypothesis that such moves would function as copulatory courtship or have another function.

The Unusual Sleeping Behaviour

The behaviour of *C. burgdorfi* males spending the night in places where the females nest is unusual among solitary bees. It is more common to observe males sleeping on branches of plants and flowers near the nesting area (Linsley 1962; Frankie et al. 1980; Alcock 1998; Alves-dos-Santos 1999; Wcislo 2003; Fraberger and Ayasse 2007). Field experiments conducted by Alcock (1998) demonstrated fidelity to the site where the males of *Idiomelissodes duplocincta* Cockerell (Apidae) slept. According to the author, one of the possible factors responsible for such behaviour could be an odour deposited in the place by the males to attract them the next night. This odour could also be one of the reasons why females do not use the galleries where males spend the night as a possible nesting site. The fact that *C. burgdorfi* males maintain a dormitory on the same site may enable males to gain quicker access to virgin females. The behaviour of entering the nests to take the females, with the associated antagonistic behaviour between males for access to females, and the great number of males flying over the aggregation when most females emerge as adults may have favoured males that sleep near nesting aggregations formed in the preceding year.

The benefits for male Hymenoptera in sleeping in groups are not yet completely understood. Thermoregulation has been suggested by some authors (e.g., Evans and Gillaspy 1964), but sleeping aggregations have also been observed in places where temperatures remained high. For example, males of *Idiomelissoides duplocincta* form large sleeping aggregations even at high temperatures during the summer in Arizona (Alcock 1998), as is also true for *C. burgdorfi* in that the nesting site is subject to high temperatures in both the day and night. Another hypothesis is that this behaviour is beneficial for defence against predators, which could mean a survival advantage for individuals in a large group (Evans and Linsley 1960; Alcock 1998). This is also controversial as it has been shown in stingless bees that sleeping in aggregation exposes males to a greater risk of predation and parasitism (Brown 1997), precisely because of the density dependent effect. This topic should be studied further as there is probably no single explanation for the phenomenon.

The behaviour of females spending the night on flowers, and away from the nest is not common. When building new nests, *Centris* females often spend the night in the nesting cavity (e.g., Gaglianone 2001; Aguiar and Gaglianone 2003; Rego et al. 2006;

Ramos et al. 2010) or in adjacent cavities that are unoccupied (e.g., Ramos et al. 2010). Despite reports of nest guarding behaviour by females after the activity period, as seen in *C. flavifrons* Friese (Martins et al. 2013), the fact that the females of *C. burgdorfi* do not spend the night in the nest site does not necessarily mean an increased susceptibility of the nest under construction to cleptoparasitic attacks, since cleptoparasites tend to be more active during the day (Wcislo et al. 2004; Kelber et al. 2005). Future studies are required to understand the advantage of locating the dormitories away from the nests and from the brood. The only source of oil resources identified in nests of *C. burgdorfi* was *Krameria tomentosa* (Silva et al. 2012), the same plant where the females spend the night. The adaptive significance of females sleeping on *K. tomentosa* is unknown, although perhaps females that choose this plant can secure floral oils from it early in the morning, before returning to their nests. This should be tested to determine if this resource is limited in the area.

Centris burgdorfi was never found nesting in other sites besides petrified dunes in Brazil. The same structure is using as nesting place by the females and as sleeping place by the males. The presence of these geological formations in the environment is of extreme importance for the maintenance of these species that require this particular structure in their life cycles. The loss of habitat has been a decisive factor in the disappearance of several insect populations which, in turn, can affect many ecosystem services.

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