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On the Production, Mating and Behavior of Males in *Synoeca surinama* (Vespidae: Polistinae: Epiponini)

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Abstract

In colonies of Neotropical swarm-founding wasps (Epiponini), males are thought to be produced only in periods when there are many queens present. Little information is available regarding male behavior in and out of the nest, and male mating strategies are poorly understood. Here, a behavioral study of males of *Synoeca surinama* is provided and copulation behavior inside a nest is described for the first time. A description of an aggregation of non-natal males at a nest is also provided. The behavior of males was observed in three colonies subjected to removal of queens for another study. Nest envelope was partially removed, and the observations were made directly (seen by "the naked eye") and indirectly (through camcorder recordings), daily. Production of males occurred in large colonies with number of workers being more relevant than the number of the queens. Males of the aggregation were marked and filmed. The aggregation of non-natal males was observed for seven consecutive days next to the largest colony; some of the males attended the aggregation on consecutive days. The males were observed accessing the comb by the opening in the envelope and courting new queens. One successful copulation on the comb of the nest was observed. In the colony where the male aggregation was observed, 47.6% of the new queens were inseminated while in the other two colonies, no new queens were inseminated. These observations suggest males are attracted to, aggregate and seek mating opportunities at non-natal colonies that are producing young adult queens.

Introduction

Studies on social wasps are mainly focused on females, queens and workers, which are responsible for the reproduction and maintenance of colony respectively. Males receive less attention, in part because of the brief period adult males remain in the nest in most species (West-Eberhard, 1969; Jeanne & Castellón, 1980; Gadagkar, 1991; Starks & Poe, 1997). Males are frequently attacked by females (O'Donnell, 1999) and are expelled from their natal nests (West-Eberhard, 1969; Kasuya, 1983). Males contribute very little to the maintenance of the colony and alter the nutritional balance, being evicted to reduce additional costs (Kasuya, 1983; Suzuki, 1986). In colonies of Neotropical swarm-founding wasps (tribe Epiponini) males are rarely seen and seem to be produced only in periods when there are many queens present (Queller et al., 1993, Boomsma & Grafen, 1991; Pamilo, 1991).

A great diversity of mating strategies is observed in Hymenoptera. Vespinae and Polistinae, independent founders, are known to have sexual pheromones produced by females to attract males and stimulate mating behavior (Downing, 1991), and pheromones produced by males to mark territory (Landolt et al., 1998). In many species, males mark territory or other points rubbing the abdomen in the substrate to attract or intercept flying females to mate, suggesting that external glands produce pheromones (West-Eberhard, 1982; Post & Jeanne, 1983; Wenzel, 1987; Beani & Turillazzi, 1988; Reed

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& Landolt, 1991; Beani et al., 1992; Beani, 1996). In other social hymenoptera, such as *Apis*, the males patrol or expect females in certain places (Alcock et al., 1978). In stingless bees (Meliponini), the males form aggregations near active nests that have young new queens (Cortopassi-Laurino, 2007).

There is little information regarding male behavior inside and outside of the nest in Epiponini and even less about mating strategies. Male aggregations distant from nests were observed in *Polybia sericea* (West-Eberhard, 1982) and *Polybia occidentalis* (Jeanne, 1991). Recently, Chavarría and Noll (2014) observed males of *Chartergellus communis* trying to enter a nest with new females, possibly seeking to copulate. However, mating *in situ* has never been observed. In this work, we provide behavioral observations of males of a species of Epiponini and describe, for the first time, copulation behavior inside the nest. A description of an observed aggregation of foreign males is also provided.

Material and Methods

The behavior of males was observed in three colonies (I, II and III) of *Synoeca surinama* (Linnaeus, 1767), located at farms in the municipality of Indiaporã, São Paulo state – Brazil (19° 59' S; 50° 18' W). These colonies were subjected to removal of queens, to investigate the production of new reproductives for another study (Table 1). The nest envelope was partially removed to stimulate construction and foraging activities.

Most workers were marked with quick-drying ink, according to the task performed. A sample of newly emerged females as well as four and 16 males, who emerged in the period, were marked in colonies I and II, respectively. Queens were captured when laying eggs and the newly emerged wasps at the time of emergence. The certainty of marking newly emerged was due to the fact that, in this period, they do not have flying ability. Males were identified based on some morphological differences as follows: antennae little longer (13 segments in males and 12 in females) and thinner, the mandibular teeth are smaller; the gena is slightly narrower with its upper ends somewhat less protruding; and the last visible gastral sternite is flattened (Richards, 1978). All resident males were marked to distinguish them from males coming from other colonies.

After marking, wasps were observed directly and on video recordings, from daily bouts (2 to 3 hours) of filming (Sony Handycam DCR-SR 85 digital camcorder) for four days, to survey the behaviors and interactions between workers, queens and newly emerged adults. One week after the beginning of observations, all queens and unmarked individuals were removed. In the following days, males and newly emerged females were marked and their behavior monitored.

At colony I, a few days after the start of oviposition, an aggregation of males formed. The aggregation was observed and filmed throughout the period in which it persisted. Number of males was estimated based on the videos and counting individually. Because males and females of *S. surinama* are very similar morphologically, a sample of 60 individuals from the aggregation was identified with the aid of a hand lens (using the morphological characters mentioned above) to confirm that the wasps observed were males. Fifteen of the 60 identified males were marked with quick-drying ink.

Demographic, behavioral and physiological data from six more colonies were used for comparisons with the colonies studied here. Spearman's correlation tests were performed, using R (R core team, 2019), to compare frequencies and for correlation analysis respectively.

Results

Behavior, interactions, and permanence of young males in colonies

Synoeca surinama males were observed performing ventilation behavior by fanning their wings at the comb, usually before self-cleaning. Also, they showed cell inspection, although they did not insert the whole head into the cells as the workers do. It is important to note that these behaviors were very sporadic in such a way that they did not contribute to the maintenance of the colony. Males remained grouped to the nest peripheries (between the comb and the inner edge of the envelope) with queens and newly emerged females.

Sporadically they walked on the comb and interacted with the workers to obtain resources by trophallaxis. However, in colonies I and II, many males were seen receiving aggression from workers, such as bites on the body and, on many

Table 1. Period of observations and demographic characteristics of observed colonies of *Synoeca surinama*.

Colony	Period of observations	Nº of queens before removal	Nº of workers at the beginning of observations	Nº of new produced queens	Days between removal of the queens and the collection of the colony	Nº of nest-born marked males
I	01/04/2012 to 02/05/2012	15	1374	84	25	57
II	11/04/2012 to 02/05/2012	18	812	56	12	53
III	10/09/2012 to 10/10/2012	28	571	38	23	69

occasions, they were held and both male and workers in struggle, fell from the nest. As newly emerged males had little ability to fly, many were seen on the ground. The number of workers was positively related with the number of males produced by a colony (Spearman's correlation rho = 0,71; N = 9; $p < 0.05$). Number of queens was not positively related with the number of males produced (Spearman's correlation rho = -0.51; N = 9; p = 0.16).

The residence time of males in the nest (adult emergence to departure) was short (no more than seven days after emergence), even in colony III, where attacks were observed. Only three of the 179 marked males in the three colonies (1.7%) were collected at the end of the observations and these had emerged only five days before the collection. On the other hand, from the 733 newly emerged females marked, 408 (55%) were collected in their natal nests. These results suggest that most males are expelled by workers a few days after emergence and/or they leave the nest permanently by themselves, to probably join mating aggregations.

Aggregation of non-natal males and mating of new queens

Eleven days after the removal of the queens in the largest colony (I), new queens starting laying eggs. Four days after the beginning of oviposition, the formation of a foreign male aggregation was observed in the tree canopy nest substrate. The aggregation was six meters high and three meters distant from the nest. We estimate more than 150 males flying nimbly and landing on the leaves of trees, where they remained for a few minutes and flew to other leaves again. Males were observed alone or in small groups (up to three) in the leaves.

As the vegetation in a radius of 50 meters was basically grasslands, males were observed only in the leaves of the tree where the nest was built. The aggregation was formed for seven consecutive days but, each day, the number of males apparently decreased. Males arrived approximately one hour before sunset and flew away to a small fragment of forest (15.000 m^2), located 300m from the nest, few minutes after the beginning of the sunrise. Some of the 15 marked foreign males were seen in consecutive days, which suggests the same males form the aggregation during various days.

We observed males accessing the comb by entering the opening we made in the envelope. Fifteen landings were observed on the comb during four days of the period in which the aggregation lasted. In 10 of the 15 landings males were immediately recognized and attacked. Nevertheless, not always the males were recognized. On one occasion a male landed and walked for about three minutes before finding a new queen and try to copulate. On five occasions they managed to mount the females but successful copulation was observed only one time since the new queens bend the gaster trying to prevent the union of the genitals. Sometimes they were noticed by the workers, who immediately attacked, seized and bit the males. Most males escaped and flew off. Several males landed without apparently being noticed. In this case, they walked across the comb directly to a new queen, who was behaviorally identified, and then attempted copulation. The males mounted the female's back, holding her with his legs, stretching their abdomen to expose the genitals and bending the end of the gaster in an attempt to unite his genitalia with that of the new queen. The observed mating behavior performed by males was similar to that observed and described by West-Eberhard (1969) for *Polistes fuscatus*.

No males were attacked when they were away from the nest, although they landed very close (within one meter) and, no sign of competition was observed among the males. Copulation attempts by resident males (belonging to the observed colonies) were not observed. In colonies II and III, no new queens were inseminated, on the other hand, in the colony where the aggregation of males was present (I), 40 of the new queens (47,6%) were inseminated and oviposition of new queens was observed only in this colony. In addition, although the establishment of a new set of queens (females with developed ovaries) occurred in all colonies, oviposition by the news queens was observed only in the colony I, the colony where the aggregation of foreign males was observed.

Discussion

In *Synoeca surinama* males are produced in large colonies, with many workers, regardless of the number of queens. This same tendency was observed in *Asteloeca ujhelyii* (Nascimento et al., 2004) and *Metapolybia aztecoides*, where the males are produced in large polygynous colonies (West-Eberhard, 1978). These three species belong to the same clade, being closely related (Wenzel & Carpenter, 1994; Pickett & Carpenter, 2010) and, it is possible that in this group the production of males in colonies with large numbers of workers (larger working force) is an adaptive strategy to minimize the risk of decline of the colonies for the costs males impose.

Concerning behaviors performed by males when they eclose, cell inspection is probably related to obtaining resources via trophallaxis with larvae (Hunt et al., 1982; Suryanarayanan & Jeanne, 2008) and the ventilation behavior is possibly a form of training of the wings. Males have weak flying ability in the first days after emergence and remain no more than seven days in the nest, being driven off by workers to avoid additional costs (O'Donnell, 1999) or leaving themselves permanently. Thus, they may need to be able to fly sooner than newly emerged females. In the social wasps of independent foundation, as *Polistes* and *Mischocyttarus,* males also leave their home nest in a few days after emergence (West-Eberhard, 1969; Gadagkar, 1991). In *Mischocyttarus drewseni*, for example, they remained in the nest for 4.8 days on average (Jeanne, 1972). In addition, newly emerged males of *S. surinama* do not accompany the females in swarming (Santos, unpublished data), as *Parachartergus fraternus* (Mateus, 2011) and *Polybia occidentalis* (Bouwma et al., 2000) males do.

Observations about the formation of aggregation of non-natal males near a nest suggest they were attracted chemically, although no sex pheromone has been chemically characterized in the subfamily Polistinae (Ayasse et al., 2001). It is highly likely the release of some volatile pheromone by new queens was perceived by foreign males at a great distance. The fact that an aggregation of males did not occur next to the colonies where oviposition was not observed corroborates this hypothesis. Possible sources of attractive components would be the poison and Dufour glands (Ayasse et al., 2001), or even the venon gland, as observed by *Polistes fuscatus* (Post & Jeanne, 1984; 1985).

Jeanne (1991) observed aggregation of males in *Polybia occidentalis* in scrub vegetation far from a nest, suggesting that mating occurs away from nests. Several young females were seen leaving and returning to the nest in this study, suggesting that mating would also occur in *S. surinama.* Chavarría and Noll (2014) observed males trying to enter a nest of *Chartergellus communis* with new females, suggesting that mating would also occur near or inside the nest. Mating in *S. surinama* may also occur within the nest, as well as outside, as we have seen males mounting and copulating with new queens in the comb. In this case, the nest envelope was partially opened, facilitating the access of males to comb, however, under natural conditions, with a closed envelope, access would have to be through the entrance at the top of the nest, which have workers watching.

Workers assault on foreign males was also documented for other species of Epiponini like *Chartergellus communis* (Chavarría & Noll, 2014) and *Polybia liliacea* (Jeanne, personal communication), suggesting that workers attack males, as if they do not recognize them as colony members, probably because they lack the same chemical signals (Pfennig et al., 1983).

Conclusions

This work contributes important information concerning production and behavioral aspects of males of *Synoeca surinama*. Copulation behavior was observed and described, for the first time, and the results suggest that mating may also occur at the comb, inside the nest. Production of males occurs in large colonies, with a large number of workers, as observed for other epiponines. Considering the lack of studies on the behavior and biology of males in Epiponini, and the wide variation within the group, we need further research on different species of this tribe to understand strategies that allow the evolution of all the complexity observed for Epiponini in terms of social organization.

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Authors contribution

All authors contributed to the study conception and design of the work. Material preparation and data collection were performed by Carlos Alberto dos Santos. Analysis were performed by Carlos Alberto dos Santos and Fernando Barbosa Noll. The first draft of the manuscript was written by Marjorie da Silva and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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