Males of Neotropical social wasps (Vespidae, Polistinae, Epiponini) recognize colonies with virgin females

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Abstract
Male behavior of Neotropical swarm-founding wasps has rarely been observed. The few published observations about male activities only describe their behavior during the short period they spend inside nests. In consequence, virtually nothing is known about what they do outside the colonies, and even less is known about mating behavior. This paper provides the first report of Epiponini males arriving at a colony with virgin females. The behavior of males and workers after queen removal was observed in one colony of Chartergellus communis located at a farm in Pedregulho, São Paulo, Brazil. The day after queen elimination, males were observed outside the nest. When males tried to enter the nest, workers aggressively attacked them. These attacks were similar to the defensive behavior used when foreign conspecifics attempt to enter the nest. The aggressive workers response and the absence of males before queen removal indicated that the males did not belong to the colony. Additionally, no fights were observed between individuals before queen removal. It is likely that foreign males arrived at the colony to mate with virgin females. Observations suggest that epiponine males are able to find nests with virgin females in mature stages of the colony cycle, and that mating can occur during different stages of the colony cycle.

Keywords
Males, social wasps, queenless, colonies
Introduction

Females are the foundation of Hymenoptera societies: queens are responsible for reproduction, and female workers perform all the tasks related to colony maintenance. Males do not play any essential social role in the colony, rather, they represent an energetic cost because they frequently request or rob food from workers (Turillazzi 1985). For this reason, workers frequently attack males and drive them from the colony (West-Eberhard 1969, Kasuya 1983). Males of social Hymenoptera usually spend little time in their natal colonies, eventually departing to search for unrelated females with which to mate (Strassmann 2001).

Males of Epiponini wasps have been observed only during certain periods of the colony cycle: in the male production phase (Noll and Zucchi 2002), during colony foundation (Richards 1978, Castellón 1982, West-Eberhard 1982, Strassmann et al. 1997), and during the swarm emigration in *Apoica* (Howard et al. 2002). These observations suggest epiponine mating may occur in newly established nests. According to West-Eberhard (1982) males could follow the scent trail of the founding swarm looking for virgin females with which to copulate. In fact, males of social Hymenoptera could be attracted by pheromones released by females, or females could be attracted by pheromones released by males in aggregations (Hölldobler and Bartz 1985, Ayasse et al. 2001). Nevertheless, some males of social wasps (like *Parachartergus colobopterus*) and bees search for virgin females around nests (West-Eberhard 1982, Boomsma et al. 2005). Regardless, the behavior of males has been poorly studied in Epiponini, and mating has never been observed for any species, so nothing is virtually known about their reproductive strategies, let alone how and where males search for females. Here we provide the first report of Epiponini males arriving at a colony with virgin females.

Material and methods

One colony of *Chatagergelus communis* was observed for six months (05/2010 to 07/2010, 09/2010 to 11/2010), twice a week, four hours a day; at a farm located in Pedregulho, São Paulo State, Brazil (20°15’S; 047°27'W (DDM), 1041 m AMSL). A section of nest envelope was cut, and put back (as a door) every day, in order to perform the observations. To identify queens, some eggs were eliminated to stimulate oviposition. All queens and a sample of workers (N=40) were individually marked with quick-drying paint. During the first month of observations 11 females were observed laying eggs. Nevertheless the number of reproductive females decreased, until one remained as the sole egg layer in a colony of 298 adults. After five months of observations (24/10/10) the queen was eliminated in order to study the behavior of workers in an orphaned colony. Before queen removal the colony never passed through a male production stage, additionally no males were observed outside or inside the colony. After queen elimination males were observed flying outside the colony, their behavior and worker response to male presence were observed for three days after queen removal.
Results

The day after queen elimination males were observed outside the colony. Males constantly tried to get into the nest (by the entrance and by the open door) inducing an aggressive response from workers. When workers perceived the presence of males, they immediately flew off the nest to face them and prevent their entrance. Workers fought aggressively against males during flight: they struck, bit, and grasped the male body. Sometimes fights were so violent that males and workers fell to the ground and continued fighting; one male was dead after an encounter with a worker. Before queen removal no aggressive behaviors were observed between colony members.

Discussion

The workers’ response against males was similar to the defense response used when foreign individuals try to get access to colonies. Aggressive behaviors toward arriving males were also observed in a colony of Polistes liliaceae in Brazil (Jeanne pers. comm) and in a colony of Vespa crabro (Bunn 1988), where workers attacked males when they tried to get inside the nest. The degree of aggressiveness shown by Chartergellus communis workers towards arriving males suggests these males did not belong to the observed colony.

Social wasps can recognize nestmates (Pfennig et al. 1983, Gamboa et al. 1986). If males do not share chemical cues from the nest (Pfennig et al. 1983), they will be attacked because workers do not recognize them as colony members. If observed males were siblings of the colony, female response probably would be different. For example, even during the colony male-production phase where workers expel males from the colony through aggressive behaviors (darts, chasing and biting), interactions never resulted in the death of males (West-Eberhard 1969, Kasuya 1983, Chavarría and West-Eberhard 2010, Chavarría unpublished data). In these cases, nest mate recognition might influence the lower level of aggression against sibling males compared to that observed against outsiders (Pfennig et al. 1983, Gamboa et al. 1986).

The observations of males arriving at the colony after queen elimination suggest males were attracted to the nest. It is possible that queen elimination stimulated some workers to develop their ovaries (Fletcher and Ross 1985) given that many of the females were observed trying to lay eggs one week after queen removal (unpublished data). Females could release pheromones or secretions from the venom gland (Post and Jeanne 1984) to signal they were receptive to copulate (Ayasse et al. 2001), attracting foreign males as a result. Something similar was observed in ants, where gynes within their natal nest “call” males that fly in search of mates (female-calling syndrome: Hölldobler and Bartz 1985). According to Boomsma et al. (2005) and Bunn (1988) males of social insects that hover around nests containing virgin females, usually copulate near to the nest. Unlike primitive social wasps, queens and potential reproductives of Epiponini wasps remain in the nest. Therefore their mating strategy could be associated
with males patrolling and searching for virgin females. These males may attracted by pheromones and they probably mate close to or inside the nest.

Our observations on *Chartergellus* suggest that mating strategies could involve the active searching for receptive females by males. Nevertheless, since epiponines show a great deal of variation in nest architecture, morphological caste syndromes, colony size, and distribution (Richards 1978), it can be expected that they also exhibit a variety of male mating strategies across species. For this reason, our observations cannot be generalized to all epiponines, nevertheless they show that males are able to find nests with virgin females in mature stages of the colony cycle. In contrast to previous findings (Ross and Carpenter 1991), our results suggest that mating in Epiponini would not necessarily occur at the time of colony foundation. This would be an important trait for colony survivorship, since in case of queen loss males could find a nest with no inseminated females and copulate, ensuring colony reproductive success. Probably mating occurs whenever a colony requires, and this may occur during colony foundation, or later in the colony cycle as West-Eberhard (1978) observed. Although more observations on male behavior are necessary, the observations reported here show that mating strategies of Epiponini could be complex, and mating can occurs during different stages of the colony cycle.

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**References**


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