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A NEW HOST ASSOCIATION OF *COMMOPTERA SOLENOPSIDIS* (DIPTERA: PHORIDAE) WITH THE ANT *PHEIDOLE DENTATA* (HYMENOPTERA: FORMICIDAE) AND BEHAVIORAL OBSERVATIONS

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Abstract

Phorid flies are well known myrmecophilic organisms and are often parasitoids of ants. In some cases, phorids live commensally with ants, with the colony offering protection and/or feeding opportunities. In this study we examined the phorid *Commoptera solenopsidis* in association with a new host species, *Pheidole dentata*. An ethogram was performed describing the fly and its association with different *P. dentata* castes. The flies spent most of their time performing grooming behaviors, allogrooming ants, or self-grooming and most commonly were associated with the major workers. We discuss the significance of this association as well as the possible evolutionary driving force behind *C. solenopsidis* having multiple hosts.

Key Words: *Pheidole, Solenopsis*, social parasitism, phorid, *Commoptera*

Resumen

Las moscas fóridos (Phoridae) son bien conocidas como organismos mirmecofilicos y a menudo son parasitoides de hormigas. En algunos casos, los fóridos viven comensalamente con las hormigas, con la colonia ofreciendo protección y/o oportunidades de alimentación. En este estudio examinamos el fórido *Commoptera solenopsidis* en asociación con una nueva especie, *Pheidole dentata*. Se realizo un etograma describiendo la mosca y su asociación con diferentes castas de *P. dentata*. Las moscas pasaron la mayoría de su tiempo acicalándose, alo-acicalándose las hormigas o acicalándose ellas mismas y fueron mas comúnmente asociadas con los trabajadores principales. Discutimos lo significativo de esta asociación y la posible fuerza motriz evolucionaría que esta detrás de que *C. solenopsidis* tenga hospederos múltiples.

Phorid flies (Diptera: Phoridae) are well known for their association with ants, often living as either nest commensals or aerial parasitoids (Disney 1994; Feener & Brown 1997; Brown & Feener 1998; Brown 1999). Parasitoids have been implicated in mediating ant competitive dynamics (Feener 1988; Orr 1992; Feener & Brown 1993; Porter et al. 1995) and have more recently been used as an attempted control agent for invasive species of ants, such as *Solenopsis invicta* (Vogt et al. 2003; Morrison & Porter 2005, 2006; Vazquez et al. 2006). The parasitic interactions between phorids and ants have thus been relatively well studied (Feener & Brown 1997; Brown 1999), but less is known about the evolution of their association and the behavior of phorids living commensally within ant nests, especially concerning non-parasitic interactions between these two groups (Hölldobler & Wilson 1990).

Commoptera solenopsidis, a small phorid fly about 1.5 mm in length, was first described in close association with *Solenopsis geminata* (Brues 1901) (Fig. 1). Although only the female has been described, these flies have only rudimentary wings and swollen membranous abdomens. Numerous *C. solenopsidis* were found within a single nest of *S. geminata*, but no other specimens were found in other ant nests of the same species (Brues 1901). From the initial description, the lifestyle of *C. solenopsidis* is unknown and neither larvae nor males have been observed, but from the limited observations there were no parasitic interactions recorded (Brues 1901). Other related phorids classified in the *Metopina*-group of genera (Brown 1992) are either predators, scavengers, or have unknown ways of life (Rettenmeyer & Akre 1968).

Here we report on a new host record of *C. solenopsidis* in association with a new ant host, *Pheidole dentata*, different from the original host description by Brues (1901) (Fig. 1b-d). In addition we report behavioral observations of this fly within *P. dentata* colonies and its association with different ant castes. We also hypothesize about the evolutionary relationship between *C. solenopsidis* and its 2 described hosts as well as how it is able to live within ant colonies.

Materials and Methods

Queenright colonies of *Pheidole dentata* containing *C. solenopsidis* were collected in Gaines-

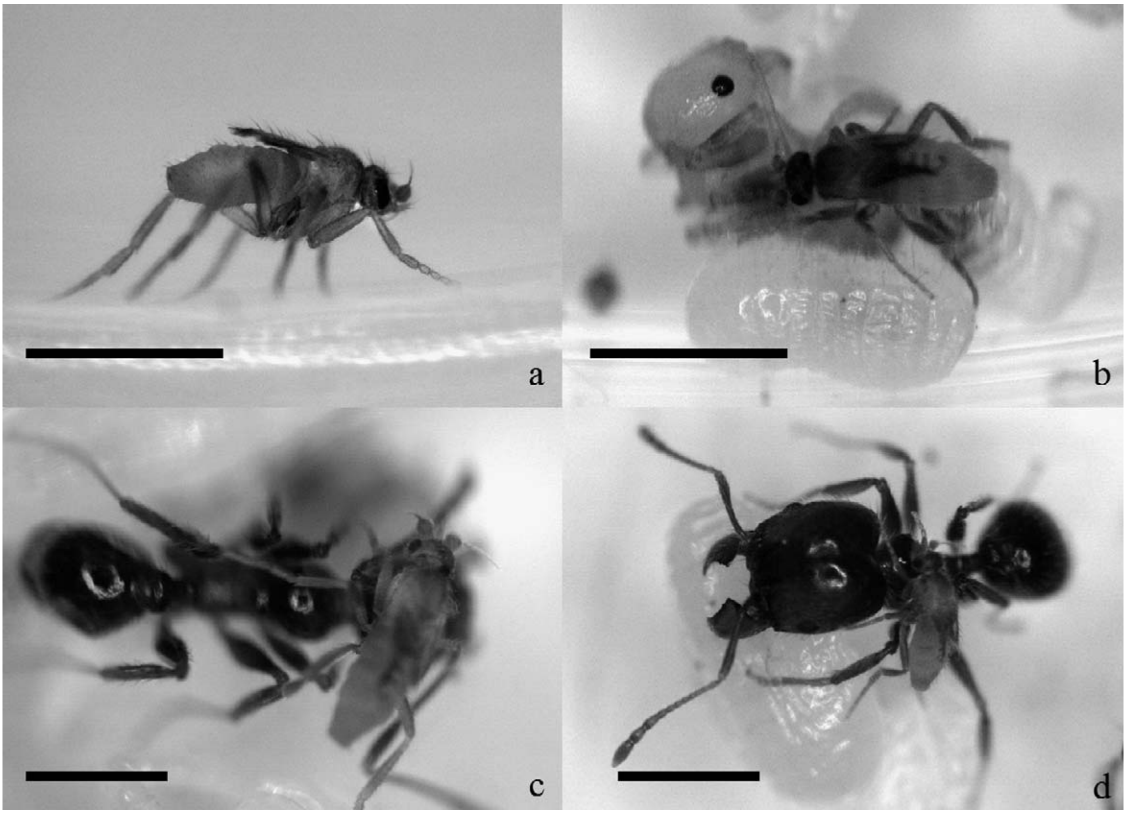

Fig. 1. (a) Close-up of *Commoptera solenopsidis*. (b) *C. solenopsidis* on a *Pheidole* pupa. (c) *C. solenopsidis* on a *Pheidole* minor worker. (d) *C. solenopsidis* on a *Pheidole* major worker. (scale bars ≈0.5 mm)

ville, FL nesting in decaying logs. *Pheidole dentata* is an ant with a dimorphic worker caste (major and minor workers, with head widths of 1.0mm and 0.5 mm, respectively). Most flies were observed after the ant colonies were brought back to the laboratory and observed under a dissecting scope, but in a few cases flies were observed in the field during the collection process. Although lab colonies never were observed to have more than 2 flies per colony, it is possible that colonies contained several individuals based on field observations.

Behavioral Observation

Three colonies of *P. dentata* containing *C. solenopsidis* were placed in dental-stone nests and covered by a thin sheet of glass. Each colony contained approximately 300-500 workers with a caste ratio of about 10-20% major workers as expected for this ant species (Seid & Traniello 2006). All colonies were reproductively active and contained brood in all 3 states (eggs, larva, and pupa) A Nikon dissecting microscope (40×) was used to observe the flies within the colony. Detailed observations were made of the fly's behavior in conjunction with behavioral observations of the ants. A total of 10 h of observations were specifically devoted to the *C. solenopsidis* (10 h total from all the colonies combined, Colony 1, 2 h; Colony 2, 3 h; Colony 3, 5 h with 1 fly in each colony). Fly behaviors were recorded at 5-min intervals to create an ethogram of all observed fly behaviors. Frequencies of the behaviors were calculated by dividing the number of observations of any given behavior by the total number of behaviors observed. The time the fly spent in association with any given caste was calculated in 5-min intervals associated with the observed behaviors. Unscheduled behavioral observations were made to confirm that no new behaviors not included in the ethogram were present, but these observations yielded no new behavioral observations and were not included in the analysis.

Results and Discussion

Sixteen principal behaviors were observed being performed by *C. solenopsidis* over the course of the study (Table 1) and they were categorized into 3 main groups: ant grooming, self-grooming, and walking on ants. These behaviors (ant groom-

TABLE 1. ETHOGRAM OF *C. SOLENOPSIDIS* BEHAVIORS. FREQUENCY OF BEHAVIORS OF *C. SOLENOPSIDIS* TOTALING ALL OBSERVATIONS FROM 3 NESTS.

	Frequency of behaviors	Frequency totals for subcategories
Self-grooming		0.358
Licking appendages	0.100	
Rubbing abdomen with appendages	0.125	
Rubbing thorax with appendages	0.075	
Rubbing head with appendages	0.058	
Allogrooming		0.284
Grooming workers	0.067	
Grooming Majors	0.175	
Grooming Brood	0.041	
Moving		0.208
Walking on worker	0.042	
Walking on Major	0.100	
Walking on Brood	0.058	
Walking on nest	0.008	
Resting		0.125
Resting on worker	0.025	
Resting on Major	0.058	
Resting on Brood	0.042	
Feeding		0.025
Trophallaxis with worker	0.017	
Anal feeding on worker	0.008	

ing, 28.3%, self-grooming, 35.8%, and walking on ants, 20%) encompassed over 80% of all recorded behaviors. Ant grooming and self-grooming collectively were the most performed task sets. These 2 task sets collectively were the most important to the flies with over 60% of their total behaviors devoted to their performance.

In the absence of morphological mimicry, myrmecophiles may rely on some type of chemical mimicry to avoid detection by the ants (Hölldobler & Wilson 1990). If this chemical code can be replicated, co-opted and/or mimicked by a host then a given ant colony may be invaded (Hölldobler & Wilson 1990). It may be that the intense allogrooming by the phorids is to obtain the odor of the colony from the ants themselves, while the self-grooming was used to spread this odor to the flies' own bodies. There was a stereotypic pattern in the order of the self-grooming; the flies would always lick their appendence before commencing rubbing of the body. The body rub usually started with the head and thorax, but was most intense and most often directed to the abdomen (the largest part of the fly). Between each bout of body rubbing, the flies usually licked their limbs again, seemingly to soak their limbs in saliva. Although many of these actions are normal behaviors of flies in general, it was the order and sequence of the behaviors that suggested this groom/self-grooming behavior may have a role for the flies to become inconspicuous in the ant colony. Only on a few occasions did worker ants antennate the flies, but no aggressive interactions were recorded and in most instances the flies were completely ignored by the ants, thus leading to the conclusion that these flies were accepted and perhaps have obtained the colony's odor.

On 3 occasions, *C. solenopsidis* were observed in possible feeding activities with the ants, 2 observations of oral trophallaxis and 1 observation of anal feeding. In the case of the oral trophallaxis observations, these occurred when the fly simply fed off the liquid ball formed as the ants were regurgitating liquid to each other. In the anal feeding observation the ant released an anal secretion during a bout of intense abdominal grooming by the fly to the ant (possibly solicitating the release) and the fly fed on the excretion. These 3 cases were the only observed possible costs that flies applied to their host ants and they seemed to be minimal. Thus, it is possible that adult flies live commensally with these ants but more research needs to be done. It is also possible that immature flies could exact a cost on the ants as parasitoids or predators, but we never observed larvae or saw any indication that parasitism or predation occurred (i.e., some type of attack by female flies on ant adults or larvae). It may be that immature flies develop in the ant refuse pile like many other myrmecophilous phorids of *Metopina*-group genera (Rettenmeyer & Akre 1968; Miller 1984) or outside of the ant colony, but further studies are needed. In no cases were we able to maintain a population of these flies, even though the colonies that had flies persisted for several brood cycles or even years after the flies had died. Also we have only found flies in colonies freshly collected from the field, never in colonies in the laboratory even when they were kept in proximity to infected colonies.

We found that *Commoptera solenopsidis* spent more time on major workers compared to time spent on brood and minor workers (Fig. 2). This differential association is interesting and may be due to the relative inactivity of majors compared to minors. Majors are often restricted in their task performance, being specialized for defense and/or food storage (Wilson 1984; Sempo & Detrain 2004; Brown & Traniello 1998; Seid & Traniello 2006). Thus, this association with relatively inactive major workers would provide the flies with a source of contact with the colony workers with less risk of being transported outside of the colony during the performance of outer-nest tasks (i.e., nest maintenance, foraging). Although brood is also relatively stationary, brood was not preferred over major because brood may not have the necessary requirements for the flies, such as access to food, possible oviposition sites, or perhaps colony odor for the flies to maintain an inconspicuous colony profile. We did not observe these phorids on the queen, even though queens almost always remain within the nest. This may be because ants tending the queen are hypervigilant, thus the flies may be more conspicuous on the queen and easily detected as intruders. Therefore avoidance of the queen would be advantageous.

Evolutionary Considerations of Host Shift

This species was first described in association with the ant host *S. geminata* colonies in 1901 (Brues 1901) and had not been seen since, until we discovered it in *P. dentata* colonies. Although phorids are sometimes known to invade other host species (Rettenmeyer & Akre 1968), it seems surprising to find the same fly in 2 different species that are neither closely related or share a common life history. It is likely that *C. solenopsidis* co-occurs with these 2 ant species due to their predator-prey relationship and we suggest that the fly originally evolved in association with *P. dentata* and was later transfer to *S. geminata* through predatory raids in which flies in *P. dentata* colonies were taken in to *S. geminata* colonies and assimilated. It may be that when *S. geminata* raids *P. dentata* colonies, *C. solenopsidis* was able to obtain the colony odor of the *Solenopsis* before being fed upon and thus facilitating this host switching.

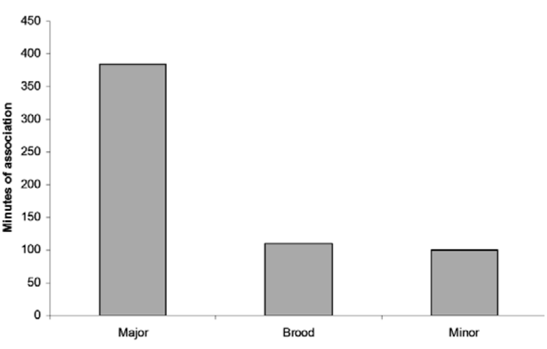

Fig. 2. Total amount of time *C. solenopsidis* spent in contact with major, minor, and brood.

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