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Phorid Flies Parasitizing Leaf-Cutting Ants: Their Occurrence, Parasitism Rates, Biology and the First Account of Multiparasitism

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Abstract
The leaf-cutting ants *Atta sexdens* (Linnaeus) and *Atta laevigata* (Smith) were parasitized by the following phorid flies: *Apocephalus attophilus* Borgmeier, *Apocephalus vicosae* Disney, *Myrmosicarius grandicornis* Borgmeier and species of *Eibesfeldtphora* Disney. The area of occurrence of phorids parasitizing *A. sexdens* was extended to include Central Brazil. The rate of parasitism on *A. sexdens* was three times lower than the rate found on *A. laevigata*; the most common flies were, respectively, *M. grandicornis* in *A. sexdens* and *A. attophilus* in *A. laevigata*. This last phorid showed the shortest life span but the higher percentage of emergence. Multiparasitism on workers of *A. sexdens* and of *A. laevigata* involving three combinations of four phorid species was rare and is here related for the first time for leaf-cutting ants.

Introduction

Diptera Phoridae represents a group of insects with large diversity of life styles during their immature stages, the majority of the larvae being parasitoids (Disney, 1994). The greater part of parasitism by these flies occurs on ants; among the genera attacked are the leaf-cutters *Atta* Fabricius and *Acromyrmex* Mayr (Feener & Moss, 1990; Disney, 1996; Brown et al., 2010), which are considered to be the most important herbivores of the Neotropical region (Della Lucia, 2011). Both host and parasitoids occur in the American continents, from southern United States to Argentina; where 28 species of attine ants are parasitized by at least 70 species of phorids belonging to 11 genera (Delabie et al., 2011; Bragança, 2011; Uribe et al., 2014), the most common being *Apocephalus* Coquillett, *Myrmosicarius* Borgmeier and *Eibesfeldtphora* Disney. This last genus was previously considered as a subgenus of *Neodohrniphora* Malloch, having being raised to the category of genus by Disney et al. (2009).

The flies usually follow and attack the leaf-cutting workers walking down their trails or in their foraging area, laying the eggs on the head or on the gaster of the host (Erthal & Tonhasca, 2000; Tonhasca et al., 2001; Bragança et al., 2002). The parasitoids may be either species-specific or may attack more than one attine species. Hosts may be parasitized by two or more species of Phoridae (Brown, 2001; Disney, 1996; Brown et al., 2010; Uribe et al., 2014). During an attack, that lasts about one second, the female seems to lay only one egg inside the hostbody where the larva will feed and develop (Bragança, 2011).

The level of parasitism of leaf-cutters by phorids generally ranges between 1 and 6% of the ants in the trails

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(Bragança, 2011).The attacks by the flies seem to have a more significant impact on foraging behavior than on mortality of parasitized ants. Real attacks or simply the flight of the flies over the ants lead to their interrupting cutting activities and fleeingto the nest, thus resulting in a reduction of available plant material as fungus substrate(Bragança et al., 1998; Tonhasca et al., 2001). The discovery of these adverse effects on ant work demonstrates a possible contribution of these flies to management of leaf-cutting ants. Several studies were conducted during the last decade aimed at increasing the knowledge of the biodiversity, geographical distribution, and biological and ecological characteristics of the parasitoid phorids, especially those concerned with *Atta* (Disney et al., 2006; Bragança et al., 2009a; Brown et al., 2010; Bragança, 2011;Guillade&Folgarait, 2011; Uribe et al., 2014).

The species *Atta sexdens* (Linnaeus) and *Atta laevigata* (Smith) show wide distribution in Brazil and are responsible for large and significant losses to agriculture and forests (Della Lucia, 2011). They are hosts of at least 10 and seven species of phorids, respectively; some of the flies can attack both hosts (Bragança, 2011). Data from the present work are part of a comprehensive research that is conducted in the savannah of Central Brazil, in the State of Tocantins, and deals with the parasitoids and the two ant species. The rate of natural parasitism was determined for both ant species. Data on occurrence were also gathered, as well more information on fliesbiology. The occurrence of multiparasitism is reported for the first time.

Material and Methods

Study area and sampling of ants

From August 2010 to August 2012, samples of ant workers were collected from trails of six colonies of *A. laevigata* and of 10 of *A. sexdens*. All were found in the municipality of Porto Nacional (10° 43' S, 48° 24' W), State of Tocantins. At the same time, samples were taken from three other colonies of *A. sexdens*, localized in the neighboring city of Palmas (10° 10' S, 48°24'W). One to two hundred ants were collected from one or two trails of each colony, at random, in intervals of 15 days, between 7:00pm and 10:00 pm, following Bragança & Medeiros (2006), although not all of the colonies were always sampled.

Rearing ants to get flies

When in the laboratory, workers of each colony were placed in a plastic tray (26 cm long, 17 cm wide), provided with a perforated lid to facilitate air flow and fed a 10 % honey solution impregnating a cotton wad that was replaced every second day. The trays and the ants were kept in climate controlled (25 °± 1°C, 80 ±5% RH and in the dark) and daily scrutinized to remove dead ants. These were individually taken into test tubes (13 mm X 100 mm) sealed with cotton and also kept in the acclimatized chambers. This procedure was adhered to for up to 15 days, at the end of which the parasitized ants are expected to be all dead (Bragança & Medeiros, 2006; Bragança et al., 2009a). In the same day of the ant's death or at most in the following day, the parasitized ants were inspected to check for the presence of phorid pupae in different parts of the host or next to it. The parasitized ants were kept in the chambers until the emergence of adult phorids. Those ants that did not show signs of parasitism were dissected to verify if phorid larvae were still inside their bodies. Emerged flies and larvae found upon dissection were preserved in eppendorf tubes containing 70% alcohol and deposited in the collection of the Course of Biological Science of the Federal University of Tocantins, in Porto Nacional, TO, Brazil.

Results and Discussion

Occurrence and rates of parasitism

A total of 66,226 workers of *A. sexdens* and 23,473 of *A. laevigata* was collected, of which 1,042 (1.57 %) and 1,258 (5.36 %) were parasitized, respectively. Workers of *A. laevigata* were parasitized by four phorid species: *Eibesfeldtphora erthali* (Brown), *Myrmosicarius grandicornis* Borgmeier, *Apocephalus attophilus* Borgmeier and *Apocephalus vicosae* Disney. These last three species were also found in *A. sexdens* but at least two other morpho species of *Eibesfeldtphora* emerged from this host (Table 1). Amongst the attacked workers, the highest rate of parasitism in *A.laevigata* was by *A. attophilus*; in *A. sexdens* it was by *M. grandicornis* whereas the least frequent parasitoids were *M. grandicornis* and *A. vicosae*, respectively (Table 1). The dissection indicated that about 2 % of the parasitized ants showed phorid larvae in their head capsules that could not be identified. Furthermore, five workers (0.42 % of all the parasitized ants) showed three combinations of multiparasitism by four species of flies, two species of the parasitoid emerging from each individual (Table 1). One *A. attophilus* fly and one of *A. vicosae* emerged from each of three workers of *A. laevigata* while one *A. attophilus* fly and one *Eibesfeldtphora* emerged from one worker of *A. sexdens*. Besides, one specimen of *A. vicosae* and one of *M. grandicornis* emerged from a single worker of *A. sexdens* (Table 1).

Most of the phorid species and of their hosts in this study can also be found in Southeastern Brazil (Disney & Bragança, 2000; Erthal & Tonhasca, 2000; Brown, 2001; Tonhascaet al., 2001). The flies *A. vicosae*, *A. attophilus* and *E. erthali* had already been found attacking *A. laevigata* in the region of Porto Nacional (Bragança & Medeiros, 2006), but this is the first time *M. grandicornis* has been found attacking that host in that zone. Thus, this work expands the list of parasitic phorids present in the savannah region of Brazil.

The data here presented corroborate other findings that indicate that the average parasitism rates on leaf-cutters by phorids generally vary from 1 to 6 % of workers on the trails (Erthal & Tonhasca, 2000; Bragança & Medeiros, 2006; Bragança, 2011), granting that it can be much higher (35%) (Folgarait, 2013), depending on the host, the fly, the site, and the time of year. The rate of parasitism in *A. laevigata* (5.4 %) was over three times that found in *A. sexdens*. Among parasitized *A. laevigata* workers, the genus *Apocephalus* (*A. attophilus* and *A. vicosae*) accounted for 81% of them, while the genera *Myrmosicarius* and *Eibesfeldtphora* prevailed in 81.3 % of the parasitized workers of *A. sexdens*. During a 12-month evaluation of parasitism on *A. laevigata* in the same region (Bragança & Medeiros 2006), the leading phorid was *A. vicosae* (68 %), while *A. attophilus* was found in only 5.6 % of parasitized workers. The reasons for these differences may be related to the sampling occasion and to variations in parasitism between the colonies of *A. laevigata* assessed and between habitats (dissimilar sampling stations). There are no reports of similar studies conducted on *A. sexdens* for further consideration.

Biology

The average survival time of ant workers parasitized by phorids is considerably smaller than that of non-parasitized ones (Bragança & Medeiros, 2006) but little is known concerning the development times of eggs and larvae. The methodology used in this work does not allow a precise determination of egg development time plus that of larval development since the date of oviposition was not known. However, the survival (in days) of the parasitized workers may offer a comparative hint of that period between the species. The survival of attacked workers, that is, the time lapse between their collection and their death, with the recognition of parasitism by discovering pupae on the host bodies or next to them (see below), amounted to only half for *A. attophilus* when compared to workers parasitized by other phorids (Table 2), thus indicating that the development period was likely only half of that of the other species. In general, the pupal period was for *A. attophilus* also shorter than that of other species. A higher emergence percentage was also found in *A.attophilus* in both hosts (Table 2). Researches conducted in laboratory under 25 ± 1ºC and 80 ± 5% UH have already shown that the time lapse from oviposition to pupal formation amounted to 9.1 ± 1.2 days for *M. grandicornis* (Tonhasca et al., 2001) and 9.6 ± 0.8 days for *Eibesfeldtphora elongata* (Brown) and *Eibesfeldtphora tonhascai* (Brown) together (Bragança et al., 2008). Similar data are not available for *A. vicosae* and *A. attophilus*, but the information from this study under similar conditions seems to indicate that this last species has the life cycle2-3 days shorter than of the phorids parasitizing both *A. sexdens* and *A. laevigata*.

After the death of all parasitized workers by *A. attophilus*, one to 14 larvae that had developed inside their head capsule left through their mouth cavity and changed to pupae far from the host, either on the tube walls or on the cotton swab. Some species of parasitic flies adjust their larval development period and only kill their host when approaching pupal formation. In this aspect, phorids of the

Table 1. Numbers and percentages of workers of two *Atta* leaf-cutter ant species parasitized by three genera of Phoridae flies (*Eibesfeldtphora*, *Apocephalus* and *Myrmosicarius*) in the central region of the State of Tocantins, Brazil. A total of 66,226 workers of *A. sexdens* and 23,473 of *A. laevigata* was collected. The larvae were found inside the bodies of the hosts during dissections. Five workers revealed cases of multiparasitism.

Atta sexdens				*Atta laevigata*			
Parasitoid	# parasitized workers	Parasitism rate (%)*	Proportional rate of parasitism (%)**	**Parasitoid**	# parasitized workers	Parasitism rate (%)*	Proportional rate of parasitism (%)**
Eibesfeldtphora spp.	253	0.382	24.28	*E. erthali*	192	0.818	15.26
M. grandicornis	594	0.896	57.01	*M. grandicornis*	18	0.076	1.43
A. attophilus	123	0.185	11.81	*A. attophilus*	758	3.230	60.25
A. vicosae	47	0.071	4.51	*A. vicosae*	261	1.112	20.75
Larvae (not identified)	23	0.034	2.21	Larvae (not identified)	26	0.111	2.07
Multiparasitism				**Multiparasitism**			
A. attophilus and *Eibesfeldtphora* sp.	1	0.001	0.09	*A. attophilus* and *A. vicosae*	3	0.013	0.24
A. vicosae and *M. grandicornis*	1	0.001	0.09				
Total	1,042	1.570	100.00	**Total**	1,258	5.360	100.00

* Regarding the number of collected ants.
** Regarding the number of parasitized ants.

genus *Apocephalus* parasitizing other species of ants may use two distinct strategies: those having short larval period, around 4-5 days, lay their eggs on wounded ants, or on those dying or recently dead. Phorids that infect healthy ants usually have a larval period of two weeks or more before pupae formation (Feener & Brown, 1997). *Apocephalus attophilus* lays the eggs inside the mouth of living workers of *A. laevigata* while they are cutting the plant (Erthal & Tonhasca, 2000). Several larvae of *A. attophilus* can developing in the ant head, and this could accelerate the consumption of the head content of the host. Thus, decreasing the survival of the host, along with a smaller larval period of this phorid compared with other flies. Minimum survival time among workers of *A. sexdens* and *A. laevigata* infected by any phorid species was only of one day (Table 2). As larvae were observed up to 24 hours after the ant's death, either inside or near the bodies, parasitized workers of *A. sexdens* and *A. laevigata* do stay alive until the end of larval development. Bragança & Medeiros (2006) have found that workers of *A. laevigata* infected by phorids kept transporting plant fragments the day before their death, thus indicating that the host does not suspend its activity of cutting when having one or more larvae inside its body.

Among other phorid genera, only one larva developed inside the body of the host. The larval development of *A. vicosae* took place inside the ant's prothorax; the rupture between pronotum and propleura exposed the pupa, thus allowing the adult emergence (Bragança & Medeiros, 2006). The behavior of this phorid during oviposition on *A. sexdens* and *A. laevigata* is as follows: the female fly walks between the workers transporting leaf fragments and jumps onto a fragment to lay the egg in the ant's mouth cavity (unpublished data). This same behavior has been described by Brown et al. (2010) as occurring when this parasitoid attacks *Atta vollenweideri* (Forel). The larva of *A. vicosae*, using a still unknown method, then migrated to the thorax to feed on the contents of the prothorax. Larva of *M. grandicornis* consumes the head content of the ant host; the pupa is found at the bottom of the capsule, under the "tentorium" (Tonhasca et al., 2001). *Myrmosicarius brandaoi* Disney and *Myrmosicarius gonzalezae* Disney, Elizalde and Folgarait, 2006 do the same when attacking *A. vollenweideri* and *Atta saltensis* Forel (Guillade & Folgarait, 2011). Oviposition by *M. grandicornis* is directed always at the right side of the host's head because of an asymmetry of the ovipositor (Tonhasca et al., 2001). Larvae of *Eibesfeldtphora* spp. develop inside the head capsule as well, devouring all of its content and locating themselves between the mandibles to pupate. Oviposition by *Eibesfeldtphora* spp. that parasitize *A. sexdens* occurs on the posterior part of the worker's head (Tonhasca, 1996; Bragança et al., 2009a) in contrast with *E. erthali*, that uses the gaster of *A. laevigata* (Bragança et al., 2002), thus indicating that the larvae somehow migrates towards the head capsule of the ant.

Table 2. Survival in laboratory of workers of the leaf-cutter ants *Atta sexdens* and *Atta laevigata* parasitized by different phorid species, the pupal duration of these species and the percent of emergence of these parasitoids. Means are shown ± SD with number of individuals in parentheses followed by the range in the next line.

Phorid	Ant survival (days)		Pupal period of parasitoid (days)		% emergence of the fly	
	A. sexdens	*A. laevigata*	*A. sexdens*	*A. laevigata*	*A. sexdens*	*A. laevigata*
Apocephalus attophilus	2.4 ± 1.0 (45) 1-5	2.8 ± 0.9 (487) 1-7	16.1 ± 2.6 (45) 12-24	16.5 ± 2.2 (487) 11-30	96.8	90.0
Apocephalus vicosae	5.3 ± 2.6 (22) 1-12	6.0 ± 1.7 (143) 1-12	19.1 ± 2.5 (22) 16-26	19.0 ± 2.3 (143) 13-30	46.8	54.8
Myrmosicarius grandicornis	5.8 ± 2.8 (228) 1-14	5.5 ± 2.1 (15) 1-13	18.8 ± 2.4 (228) 15-32	16.0 ± 1.4 (15) 15-28	38.4	83.3
Eibesfeldtphora erthali	-	4.5 ± 2.0 (79) 1-11	-	24.1 ± 4.8 (79) 8-34	-	41.1
Eibesfeldtphora spp.	5.2 ± 2.7 (162) 1-11	-	22.9 ± 2.1 (162) 17-30	-	64.0	-

(-) No parasitic relationship

Multiparasitism

From a total of 89,699 workers collected five (0.0055%) exhibited multiparasitism and the emergence of two parasitoid species (two individuals) per host (Table 1). In the multiparasitism by *A. Attophilus* and *A. vicosae* in *A. laevigata* and by *A. vicosae* and *M. grandicornis* in *A. sexdens*, the parasitoid larvae developed in different parts of the host body; thus indicating no competition among them for the food resource. However, the phorid larvae *A. attophilus* and *Eibesfeldtphora* sp. which multiparasitized the worker of *A. sexdens* (Table 1) occupied the host head capsule simultaneously, sharing the food resource and completing their development at the same time. *Eibesfeldtphora* sp. was perhaps the first to lay its egg, seeing that its development average period is longer than that of *A. attophilus* (Table 2).

A number of phorid species show inclination for attacking workers at different sites along the trails or in the foraging area; they may also show distinct attack behavior (Erthal & Tonhasca, 2000; Tonhasca et al., 2001; Bragança et al., 2009a). Phorid females seem to be attracted to their hosts by chemical and visual signals. Brown (1991) and Morrison & King (2004) offered evidence that phorids infecting other genera of ants use alarm pheromone clues to locate their hosts. On the other hand, visual stimuli from *A. sexdens* were sufficient to trigger *Eibesfeldtphora* to detect and recognize a host, although the stimuli related to the presence of a trail pheromone increased the period spent inspecting the host, thus increasing the probability of successful attack (Gazal et al., 2009).

The procedure for discriminating between parasitized and non-parasitized ants by the fly may be imperfect, bearing in mind that super parasitism has already been described both in the field and in the laboratory. Feener & Brown (1993) found a 19% incidence of natural super parasitism in *Atta cephalotes* (Linnaeus) by *Eibesfeldtphora curvinervis* (Malloch); Bragança et al. (2009b) reported rates of 29.4 %of "self superparasitism" and 49.5 % of "conspecific super parasitism" on *A. laevigata* by *E. elongate* in laboratory experiments. In both situations super parasitism was confirmed by atypical behavior during oviposition or by the presence of more than one egg or larva in the body of the host; however, only one fly emerged in these studies. The development of more than one fly of *A. attophilus* inside the host´s head, including *A. sexdens* and *A. laevigata*, seems to be not a true super parasitism because the larvae were all in the same stage and the flies appeared within nearly the same day, thus indicating that they were not product of independent ovipositions.

The only known instance of multiparasitism by phorid on ant was reported by Brown (1999). That author wrote that the phorids *Rhyncophoromyia maculineura* Borgmeier and a species of *Diocophora* Borgmeier emerged from the gaster and the leg, respectively, of a single individual of *Camponotus sericeiventris* Guérin. Although several species of phorids may be commonly seen attacking at the same time a particular colony of *Atta* (Marcos Bragança, personal observation), multiparasitism had yet not been described as occurring in leaf-cutters, be it by consecutive attacks of distinct phorids on a same ant or by watching two or more species of phorids emerge from the same ant. The low level of multiparasitism here described (0.0055% of all the collected ants) shows that this phenomenon is rare among leaf-cutters and denotes only the cases when two flies from different species come out from the same host. The rates of multiparasitism described between *A. attophilus* and *Eibesfeldtphora* sp. (0.001%), between *A. vicosae* and *M. grandicornis* (0.001%) and between *A. attophilus* e *A. vicosae* (0.013%) (Table 1) were lower than the probability of multiparasitism predicted to these three combinations (0.070%, 0.063% and 3.591%, respectively). The successful multispecies events should only occur when the larvae happen to mature at the same time. However, when multiparasitism is reckoned as the oviposition of eggs by more than one fly species on the same individual, the real incidenceof the event here described may be higher, if female flies make mistakes in host recognition (already infected or not) as frequently as in the case of super parasitism in *Atta* (Feener & Brown, 1993; Bragança et al., 2009b). Hence, cases of more than one fly emerging from an ant should be interpreted as accidental events.

The results from this work enlarge the range occupied by phorids that attack *A. sexdens* to include the savannah of South America.They also allow assessment to be made on parasitic behavior between *A. sexdens* and *A. laevigata*, the two most important species of leaf-cutting ants damaging forest and farms in Brazil. The proportional percentage of parasitism of around 60% of *A. sexden* worker ants by *M. grandicornis* and of *A. laevigata* by *A. attophilus* suggests that these two parasitoids should be the main subject of future studies aimed at the use of phorids for the management of leaf-cutting ants in Brazil. This is especially true for *A. laevigata*, with the highest parasitism rate and its primary parasitoid with the lowest larval development time and higher rate of emergence. The small occurrence of multiparasitism by phorids, here related for the first time as occurring in leaf-cutting ants, gives rise to questions having to do with the peculiarities of the host that have still to be clarified as to attraction, recognition and discrimination between hosts.

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