More studies are needed comparing interactions between *Crematogaster brevispinosa* and other *Pseudomyrmex* species. To examine the possibility that *Crematogaster* ants are colonizing heavily damaged or dying trees, the amount of herbivory over time should be quantified. Future studies should examine tree occupancy by *C. brevispinosa* and how this changes over time. Specifically, are trees previously inhabited by *Pseudomyrmex* being invaded by *C. brevispinosa,* or does *C. brevispinosa* simply colonize trees abandoned by *Pseudomyrmex*?

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Parasitic Phorid Flies (Diptera: Phoridae) Associated with Army Ants (Hymenoptera: Formicidae: Ecitoninae, Dorylinae) and their Conservation Biology[1]

Key words: parasitoids; hosts; natural history.

The most abundant insects living as guests or myrmecophiles within colonies of army ants are tiny flies of the family Phoridae (Rettenmeyer & Akre 1968).

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TABLE 1. *Observations of phorid flies attempting to oviposit in army ant workers (all observations by BVB and DHF).*

Ant	Phorid	Location
Neivamyrmex nigrescens	*Dacnophora pectinatus* Brown	Upper White Rock Cmpgd, AZ
	Cremersia sp.	
Nomamyrmex hartigii	*Cremersia* sp.	Barro Colorado Is, Panama
Labidus praedator	*Dacnophora* sp.	Zurquí de Moravia, Costa Rica

IT IS REMARKABLE THAT ALTHOUGH THIS STATEMENT was made almost thirty years ago, and in spite of steadily increasing interest in ant biology, the importance and diversity of phorid flies associated with army ants is still poorly understood. Recent books on ants in general (Hölldobler & Wilson 1990) and army ants in particular (Gotwald 1995) pay scant attention to these ubiquitous flies, citing in passing only the species that are known to live within ant colonies, which have been studied in relatively great detail (Rettenmeyer & Akre 1968). In contrast, field workers have overlooked a large and important group of phorids associated with army ants, namely those parasitic species that frequently are present during raids. In fact, Rettenmeyer (1961) stated that "Phoridae are not ordinarily taken flying about the swarm raids." We have found hundreds of specimens of phorid flies in such circumstances, however, as we explain below.

TYPES OF ASSOCIATION.—In general, there are two types of associations between phorid flies and ants (Borgmeier 1928; Brown 1993): (1) **Nest symbionts** live in ant colonies as scavengers in refuse piles, as predators of host ants, their brood or other guests, or on food regurgitated directly to them by host ants (Rettenmeyer & Akre 1968). The majority of these symbionts are associated with New World army ants (subfamily Ecitoninae). They are not discussed in detail in this paper. (2) **Aerial parasitoids**, in contrast, live independent of ant colonies as adults and are obligate parasitoids of arthropods, mostly sterile worker ants or, more rarely, reproductive females. Many of these parasitoids are extremely host specific, attacking only particular species or castes. Eggs are deposited in the head, thorax or abdomen of host ants and larval development proceeds therein. Parasitic phorids are known for many ant groups, including army ants, leaf-cutter ants (*Atta* and *Acromyrmex* spp.), fire ants (*Solenopsis* spp.), and carpenter ants (*Camponotus* spp.) (reviewed by Disney 1994).

AERIAL PARASITOIDS OF ARMY ANTS.—All previous summaries of the literature on army ant-phorid interactions have assumed that co-occurrence of the ants and flies implies a host-parasite relationship. Actual observations of phorids attacking ants, however, are exceedingly rare, and in their absence such assumptions are highly questionable. Actual host-parasite relationships cannot be gleaned from the literature, as all published records refer to flies "associated with" ants or "flying over" ants. No records of attacks on army ants are available in the literature.

Definitive records of phorids attacking army ants therefore are limited to those presented here (Table 1). Only species of *Cremersia* and *Dacnophora* are confirmed army ant parasites; these two genera are associated exclusively with non-*Eciton* army ants (Table 1). But most of the phorids we have collected in association with army ants were with the commonly observed, above-ground foraging army ant species *Eciton burchelli* and *E. hamatum*. This leaves open the following question: what are the majority of these flies doing?

PHORIDS ATTACKING VICTIMS OF ARMY ANT RAIDS.—Our observations indicate that most of the phorid species associated with raids actually attack victims of army ants rather than the army ants themselves. These victims, usually other ants, are emitting distress pheromones, substances that are known to attract some parasitic phorid flies (Brown & Feener 1991; Feener et al. 1996). Records of flies attacking the ant victims of army ant raids are summarized in Table 2.

Besides these records, we have observational data on many other parasitic phorids that we have found

[1] The latest review of parasitic phorids associated with army ants (Disney 1994) contains some small errors. Brown (1993) is cited as observing *Borgmeieriphora kempfi* with army ants, whereas no such observation was recorded. Disney also refers to "*Eciton coecum*," an old name for *Labidus coecus*, and "*Eciton schlechtendali*," a synonym of *Nomamyrmex hartigii*. These two nomenclatural problems affect the numbers in his Table 3.4. Additionally, there are some incorrect numbers in table 3.4 not due to these problems: mean number of ant species per fly species for *Acanthophorides* should be 0.4 (not 1.0), that for *Dacnophora* should be 1.5 (not 1.0) and that for *Diocophora* should be 2.0 (not 1.5).

TABLE 2. *Observations of phorid flies attempting to oviposit in host ants being raided by army ant workers.*

Host	Army ant	Phorid	Location	Reference
Camponotus crassus, C. rufipes, C. cingulatus	*Nomamyrmex esenbeckii*	*Diocophora disparifrons*	Itatiaia, Brazil	Borgmeier 1959
Solenopsis geminata	*Eciton* sp.	*Pseudacteon* spp.	Sante Fe, Panama	(DHF, new)
Gnamptogenys bispinosa	*Eciton vagans*	*Apocephalus* sp. 21	La Selva, Costa Rica	(BVB, new)
Pseudolasius sp.	*Aenictus fergusoni*	*Pseudacteon* sp.	Khao Yai NP, Thailand	(BVB, new)
Pheidole sp.	*Eciton rapax*	*Apocephalus* sp.	Pakitza, Peru	(BVB, DHF, new)
Pheidole sp.	*Eciton hamatum*	*Apocephalus* sp.	Pakitza, Peru	(BVB, DHF, new)
Pheidole subdentata	*Neivamyrmex nigrescens*	*Apocephalus* sp. 29	Peña Blanca Lake, AZ, USA	(BVB, DHF, new)
Pachycondyla obscuricornis	*Eciton lucanoides*	*Apocephalus* sp. 84	La Selva, Costa Rica	(BVB, new)

with army ants, discussed below under each phorid genus. For each genus we give the number of described species, although these numbers are probably extreme underestimates of the true number in existence.

Acanthophorides (7 described species): These flies are found exclusively associated with army ants. They are found at the raid front, often in large numbers, but their hosts are unknown. Males commonly aggregate on leaves near the raid, whereas females hover persistently over the ants.

Apocephalus (125 described species): Over forty species of *Apocephalus,* including many undescribed species, have been collected over army ant raids. They have been found associated with *Eciton burchelli, hamatum, lucanoides, mexicanum, quadriglume, rapax* and *vagans, Labidus coecus, praedator* and *spininodis, Neivamyrmex cristatus* and *nigrescens,* and *Nomamyrmex esenbeckii.* Often, they are the most abundant phorids at the raid front. In particular, we have collected hundreds of specimens of *Apocephalus* sp. 49 and sp. 50 with large raids of *Eciton burchelli* at La Selva. Although these two species are common in association with army ants, they have rarely (sp. 50) or have not (sp. 49) been collected in Malaise traps (see Brown & Feener 1995), indicating that they might be obligate army ant associates that are unlikely to stray far from raids of their hosts. Their hosts are unknown, and like *Acanthophorides* species, they congregate at the largest aggregations of ants at the extreme raid front.

Also commonly associated with *Eciton* spp. is the widespread group of species related to *A. cultellatus* (Brown 1997). We have witnessed possible oviposition attempts of these flies towards *Eciton vagans* and *E. burchelli,* but still have not observed definite attacks.

Most other species of *Apocephalus* associated with army ants probably are parasites of other ants (Table 2), but detailed observations are necessary to verify this on a case by case basis. For instance, of the three *Apocephalus* species collected over *Pheidole* sp. raided by *E. rapax* (Table 2), one species, *Apocephalus* species 15, was also collected over baited *Pheidole* in the absence of army ants. Similarly, *Apocephalus* sp. 29, which we collected over a raid of *N. nigrescens* is commonly attracted to aggregations of *Pheidole subdentata* at baits. These two species, at least, apparently are not limited in their activities by the presence or absence of army ants.

Borgmeieriphora (4 described species): We have found the small, wingless females of this genus associated with booty-laden, colony-bound workers of *Eciton burchelli* (*B. multisetosa*) and *E. hamatum* (*B. greigae*; the ant in this association was recorded as *Eciton* sp. by Brown 1993; Disney 1994). There are no association records for *B. leptotarsus,* and contrary to Disney (1994, p. 77), there are none for *B. kempfi,* either. On two occasions, at Pakitza and La Selva, we saw male *Borgmeieriphora* hovering over the inbound ants, sometimes carrying the flightless females (Brown 1993).

Cremersia (15 described species): Females of some species have been observed to attack non-*Eciton* army ants (Table 1). DHF observed that oviposition attempts were directed at the abdomen of hosts. No other specific information is available.

Dacnophora (6 described species): We have seen two unequivocal attacks on non-*Eciton* army ants by species of this genus (Table 1); others are recorded as being associated with various ants (Disney 1994). The single recorded Nearctic Region species, *D. pectinatus,* is collected frequently at blacklight traps around dusk. It is probably mostly crepuscular, as is most of the activity of its host, *N. nigrescens* (Schneirla 1971), although we once collected this species attacking ants at around 1000 h on a cloudy day. To attempt to capture other similarly nocturnal parasitic phorids, we operated blacklight traps near nocturnally emigrating and raiding army ants in Peru. Our attempt was largely unsuccessful, as the traps collected mostly nest symbionts. More collecting effort of this type is needed before this technique can be dismissed, however.

Diocophora (10 described species): One species of this genus, *D. appretiata,* is a common associate of *Eciton burchelli.* Females perch over columns dominated by inbound, booty-laden workers. In spite of hours of observations, we have seen no unequivocal oviposition attempts. All other species of *Diocophora* with known life histories are parasitoids of *Camponotus* spp., and it is possible that *D. appretiata* is simply waiting for *Camponotus* booty to be brought back by raiding army ants.

Myriophora (10 described species): BVB has collected many specimens of *Myriophora* species over raids of *Eciton burchelli* and *Labidus praedator* as well as over a raid of a *Gnamptogenys* species (not an army ant) carrying a millipede. These flies likely were attracted to the defense secretions of myriapods being attacked by the ants. A similar response can be elicited by crushing the myriapods in the absence of ants.

Pseudacteon (41 described species): DHF has observed species of *Pseudacteon* as they attacked *Solenopsis*

geminata workers that were being raided by an unidentified army ant. Similarly, BVB has collected *Pseudacteon* specimens over raids of *Labidus praedator* at Bilsa Biological Station in Ecuador.

A more specific association was observed by BVB at Khao Yai National Park, Thailand, where *Pseudacteon* females were attacking *Pseudolasius* sp. workers that were being raided by *Aenictus fergusoni.* This is our only non-New World record of opportunistic phorid parasitism at an army ant raid.

Obligate and Facultative Associates, and Conservation Biology.— Army ant colonies are important habitats, or "keystone resources" for hundreds of species of obligate and facultative associates, and their raids provide food for a large guild of ant-following birds (Willis & Oniki 1978), butterflies that feed on ant-bird droppings (Ray & Andrews 1980), parasitic flies that attack insects flushed by the ants (Rettenmeyer 1961), staphylinid beetles that prey on ants and ant larvae, or are scavengers (Akre & Rettenmeyer 1966) and many other organisms (summarized by Kistner 1982) that interact with the ants in various ways. Ant birds, in particular, have been shown to be either obligatively or facultatively associated with the ants, disappearing when the ants disappear in proportion to their dependence upon them (Harper 1989).

In a similar way, the assemblage of parasitic phorid flies associated with army ant raids might consist of both obligate and facultative associates. Some phorids probably use army ant raids only by accident; for example BVB observed several individual phorids of the species *Neodohrniphora curvinervis* attacking a column of leafcutting ants (*Atta cephalotes*) that was piling up in response to an army ant column blocking its trail. Although the flies in this instance were clearly using the fortuitous aggregation as a prime hunting ground, they normally attack *Atta* workers when army ants are not present (Feener & Brown 1993).

Species of the genera *Cremersia* and *Dacnophora* probably are obligate ant associates. Loss of army ant colonies from small patches of habitat would cause the immediate loss of these insects as well. Flies like *Acanthophorides* spp., *Borgmeieriphora* spp., *Diocophora appretiata* and *Apocephalus* sp. 49 might be obligate associates, found only with or near army ants. They might be parasites of the army ants themselves, or might attack some other obligate army ant associate.

Other phorids, especially those in Table 2, might rely only partly on army ant raids. Like some ant-birds, some phorid flies might be able to forage partly without army ants, but might still rely on ant raids to furnish them with large numbers of hosts. It has been determined that colonies of *Eciton burchelli,* a common, swarm raiding army ant, require 30 hectares of land (Lovejoy et al. 1986) in which to forage; anything less and the ants disappear. In reserves of 100ha, 3 such colonies can be expected to occur, but because of the complexities of their life cycles (Schneirla 1971; Gotwald 1995) there are times when individual colonies are not foraging. If these non-foraging days occur in coincidence, and hosts for the parasitic phorid flies are not otherwise available, populations could founder. Further experiments of the type done by Harper (1989) with birds are necessary to assess the full importance of army ants for maintaining tropical insect diversity. Additionally, we need to know more about army ants other than *Eciton burchelli,* which might need larger or smaller reserve sizes, and which might or might not be suitable surrogates for *E. burchelli.*

Although most of the attention has focussed on the effects of army ant absence on bird species (Lovejoy et al. 1986), the potential loss of species of small insects associated with these ants is of a much greater magnitude. If, as conservation biologists, we are in the business of saving species, we must save army ants, not for the few birds, but for the legions of mites, beetles, flies, springtails, wasps, bristletails and butterflies that are part of the army ant biome.

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Active Role of Two Ponerine Ants in the Elaboration of Ant Gardens[1]

Key words: Ant gardens; epiphytes; French Guiana; Ponerinae; seed dispersal.

The ants of the subfamily Ponerinae generally are considered to be primitive on the basis of morphological criteria (numerous species have retained some ancestral morphology of wasps) and their social

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