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The Effect of Foraging Army Ants on Leaf-Litter Arthropods¹

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ABSTRACT

The effect of *Eciton burcbelli* army ants (Hymenoptera: Formicidae) on leaf-litter arthropods was studied at Finca La Selva, Costa Rica. Analyses of leaf-litter samples indicated that both arthropod abundance and the number of taxa were reduced following the passage of foraging army ant swarms. Many of the arthropods in the path of an ant swarm escape; the escape tactics that we observed are presented. Full evaluation of the impact of army ant swarms on the arthropod community requires quantification of the rates of capture by both the army ants and the associated swarm-following birds, and of the rate of parasitization by flies that follow the ant swarms.

ECITON BURCHELLI (FORMICIDAE: ECITONINAE) IS A COMMON, swarm-raiding army ant of the neotropical forests; its foraging swarms cover a broad area and capture a wide diversity of arthropods. Because colonies of *E. burcbelli* have a large daily intake of food, they presumably have a substantial impact on litter arthropods in the areas in which they forage (Wilson 1971, Rettenmeyer *et al.* 1983). Their effectiveness in prey capture is not clear, however. In an early publication, Schneirla commented that they "clear insect life rather completely from terrain over which they pass" (1934, based partly on observations of Bates 1863 and Belt 1874). More recently, Schneirla (1949, 1971) and Rettenmeyer (1963) estimated that 30–50 percent of the litter arthropods escape *E. burcbelli* swarms. In a study of tropical leaf-litter arthropods, Williams (1941) analyzed the fauna from two plots the day after they were raided by army ants *Labidus praedator* and indicated that arthropod densities were reduced to "a minimum." Franks (1982a, b; Franks & Bossert 1983; Franks & Fletcher 1983) has studied the effects of *E. burcbelli* ants on leaf-litter communities in detail; his results will be referenced below when appropriate. In this study, we investigated the impact of foraging *E. burcbelli* by measuring the densities of leaf-litter

arthropods before and after the passage of army ant swarms.

METHODS

The study was conducted on 6 July and from 14–17 August 1981 at Finca La Selva, a field station of the Organization for Tropical Studies in the wet forest of the Atlantic lowlands, Heredia Province, Costa Rica (10°25'N, 83°58'W). We located swarms of foraging army ants visually and audibly by listening for the calls of birds associated with them (Johnson 1954, Rettenmeyer 1963).

Ten to fifteen meters in front of each advancing army ant swarm, we established two 1-m² plots, 1–3 m from each other, which contained approximately equal amounts of leaf litter and vegetation. These two plots were designated the "Before" plot (before ant arrival) and the "After" plot (after ant foraging). We placed a 13-cm-high square wooden frame around the "Before" plot to prevent arthropods from leaving the plot, then collected all leaf litter and arthropods into a plastic bag and removed the wooden barrier. Immediately after the army ant swarm had passed through the area, we placed the barrier around the nearby "After" plot and repeated the collection procedure. In the laboratory we searched through the litter samples and collected, stored in alcohol, and identified the arthropods to Class, Order, or Family. We dried the stored arthropods at 60°C for two days, then

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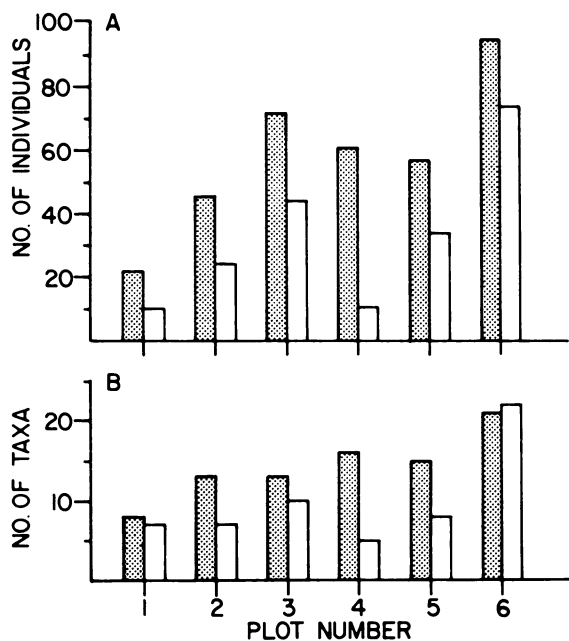


FIGURE 1. Arthropod populations (A) and diversity (B) of six matched pairs of 1-m² leaf-litter samples taken before (shaded bars) and after (unshaded bars) the passage of a foraging swarm of army ants (*E. burchelli*).

weighed them to estimate the arthropod biomass of each plot. Our observations include data from six matched-pairs of "Before" and "After" plots.

On 6 July 1981, a larger group of observers (see list in Acknowledgments) at the front of a swarm raid of *E. burchelli* recorded escape tactics employed by litter-inhabiting organisms.

RESULTS AND DISCUSSION

We collected a total of 548 arthropods from six pairs of litter plots and separated them into 47 taxa. More arthropods were present in the plots before the army ants arrived than after they had foraged (Fig. 1; Wilcoxon's matched-pairs signed-ranks test [WSRT], $P < 0.025$). Fewer taxa were found in five of the six pairs of plots after the army ants had passed through them (Fig. 1); this reduction in number of taxa was also significant (WSRT, $P < 0.05$). The differences in the biomass estimates were not significant because of high between-plot variation in biomass measurements. For the four most common taxa, which represent two thirds of the arthropods collected, the number of individuals collected from "After" plots was generally less than that from "Before" plots (Fig. 2); however, these differences were statistically significant only for Isopoda and Chelonethida (WSRT, P

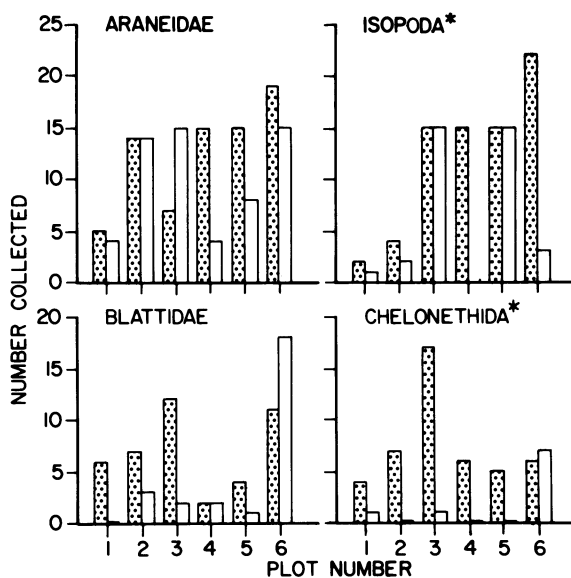


FIGURE 2. Populations of the four most common arthropod taxa collected from six matched pairs of leaf-litter samples taken before (shaded bars) and after (unshaded bars) the passage of a swarm of foraging *E. burchelli*. An asterisk indicates that the number of individuals collected was significantly lower for that taxon after army ant foraging ($P > 0.05$; Wilcoxon's matched-pairs signed-ranks test).

< 0.05). These quantitative data support the statements made by Rettenmeyer (1963) and Schneirla (1971) that, although swarms of *E. burchelli* appear to completely search the areas they forage in, they do not capture all the potential prey in their paths. For example, cockroach abundance was reduced by 38.1 percent. This is similar to the 50-percent reduction in cockroaches noted by Franks (1982a).

The high variability in arthropod numbers and diversity from "Before" and "After" litter plots probably reflects the nonhomogeneous distribution of arthropods on the forest floor (compare the values in the "Before" columns of Fig. 1). By selecting similar plots in close proximity we tried to reduce this source of variance. Differential foraging by the ants on or near the "Before" and "After" plots could have also increased the variance in the results. We partially compensated for this by not sampling from within or near plots where the ants obviously foraged dissimilarly on the "Before" and "After" plots.

An organism in the path of an army ant swarm will experience one of three possible fates: direct predation by army ants, subsequent predation or parasitization by other animals, or escape to overhead vegetation, laterally out of the path of the ant swarm, or down into the leaf litter. Although our leaf-litter analyses do not differentiate among

TABLE 1. *Arthropods observed at the front of a foraging swarm of E. burchelli, the number caught, and their reactions to the army ants.*

Order	Common name	Number observed	Number captured	Reaction to army ants
Orthoptera	Cockroach			
	Nymph, small	3	2	run, jump, hide
	Nymph, large	11	3	run, jump, hide
	Adult	5	0	run, fly, hide
	Cricket	12	5	jump, walk
	Walking stick	1	0	motionless, ignored
Hymenoptera	Ants			
	<i>Ectatomma ruidum</i>	12	6	nest evacuation, hide, run, drop off vegetation
	"Tiny ants"	10	3	walk
	<i>Atta</i> colonies	3	0	ignored
	<i>Paraponera</i> colonies	2	0	ignored
	Bee	1	0	fly
Trichoptera	Caddis fly	2	0	hide up on vegetation
Coleoptera	Beetles	3	0	ignored, jump, walk, hide
Dermaptera	Earwig	1	0	climb up stem
Diptera	Fly	3	0	fly
Lepidoptera	Moth	2	0	fly, hide
Isopoda	Pillbug	1	0	run
Araneida	Spiders	27	0	run, jump, hide

these three possibilities, we observed that about 80 percent of the organisms at the front of the swarm escaped the army ants (Table 1). We did not observe *E. burchelli* catching spiders, beetles, or flies. Crickets and cockroaches were captured fairly frequently (42% of crickets, 36% of cockroach nymphs, but no winged adult roaches). Ant nests were regularly invaded with heavy losses of larvae and pupae, but adults often escaped by running up into the vegetation. Interestingly, *E. burchelli* appeared to avoid *Atta* and *Paraponera* ants completely. With the exception of spiders and *Paraponera*, our observations are in agreement with those of Rettenmeyer (1963) and Rettenmeyer *et al.* (1983).

Those arthropods that escape direct capture by army ants may be killed subsequently by the birds or parasitoids that follow army ant swarms. The ant-following antbirds (Formicariidae), along with woodcreepers (Dendrocolaptidae) and other bird species, catch numerous spiders and insects, both in the vegetation above the ants and from among the ants themselves (Johnson 1954; Schneirla 1956; Rettenmeyer 1963; Willis & Oniki 1978; Franks 1982a; pers. obs.). Some of these arthropods are flushed from the leaf litter, others from the overhead vegetation. Franks (1982a) estimated that these birds eat nearly twice as many nonant arthropods as the army ants themselves do. Additionally, parasitic flies (Tachinidae and Conopidae) that are nearly always present with *E. burchelli* swarms (Rettenmeyer 1961, pers. comm.) parasitize 50–90 percent of the cockroaches and crickets that flee from the

ants (Rettenmeyer 1961). These flies undoubtedly parasitize some of the arthropods that are subsequently eaten by birds, as well as some that escape both the ants and birds (*i.e.*, arthropods in our "After" litter plots). The various possible fates of leaf-litter arthropods are depicted in Figure 3. The size of each cell indicates the relative number of arthropods that suffer this particular fate, based on this study, Franks (1982a), and Rettenmeyer (1961).

The local abundance of arthropods in leaf litter may influence the behavior of the foraging ants. We supposed that high ant densities and slow advance of the ant swarms were associated with high prey density, but we were unable to quantitatively document these relationships. The ants' foraging behavior may be facultatively adjusted to prey densities simply through their recruitment behavior (Chadab & Rettenmeyer 1975). Rettenmeyer (1963) suggested that, perhaps because of mutual stimulation among workers, larger groups of army ants are more efficient at capturing prey than smaller groups are. This would be particularly true for large prey, colonies of other social insects (Chadab & Rettenmeyer 1975), and for prey occurring at high densities. Prey abundance may also influence emigration frequency and distances moved during emigrations (Topoff & Mirenda 1980). Similarly, there may be an interaction between prey abundance and colony food demands that influences the frequency and area of swarm raids. For example, during the starchy phase when colony demand for food is low, *E. burchelli* raids cover a mean distance of 89 m and occur on about 13

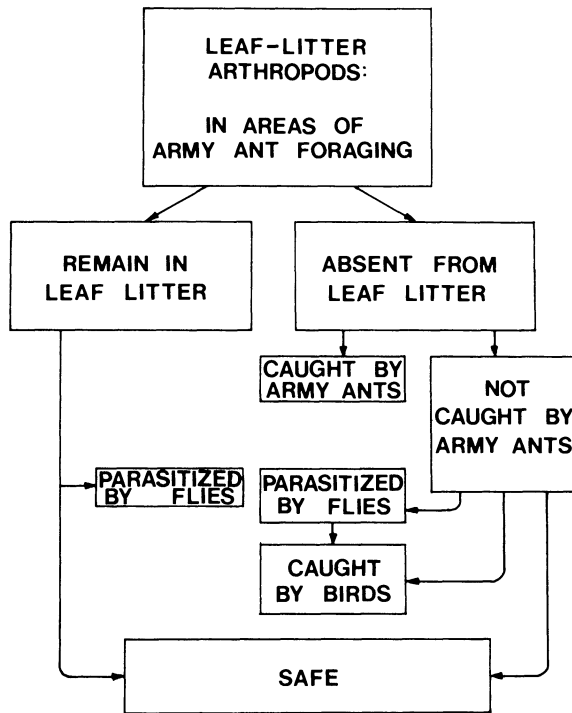


FIGURE 3. Flow chart of the potential fates of leaf-litter arthropods in the path of foraging *E. burchelli* ants. Leaf-litter arthropods are affected by the probability that army ants will forage in a given location, by predation by army ants and birds, and by parasitism by flies. The size of a cell in the figure indicates the relative number of arthropods that suffer that particular fate.

of every 20 days. During the nomadic phase, when there is a new brood of callow adult ants and larvae are present in large numbers, emigrations occur daily and raids cover an average distance of 116 m (Franks 1982a, Franks & Fletcher 1983). Franks (1982b, Franks & Fletcher 1983) studied an *E. burchelli* colony introduced to a small island previously free of army ants and with a high density of nests of ant prey species. Although the proportion of the ant brood that was captured increased dramatically, the characteristics of the swarm raids remained essentially the same, which contradicts the hypothesis that prey densities influence ant raids. Experimental manipulation of prey densities encountered by both small and large swarms of *E. burchelli* are needed to clarify the effect of prey abundance on swarm behavior and the effectiveness of prey capture by swarms of different sizes.

Most arthropods exhibit strong reactions to army ants or their pheromones. The means of escape used by other arthropod species were variable (Table 1), but most of the nonsocial species remained motionless until discovered by the ants, then moved rapidly to escape the ants and

the associated birds and parasitic flies. A stick insect (Phasmidae) escaped by remaining motionless; phasmids and some other arthropods have chemical substances which repel army ants (Schneirla 1956). Polistine wasps (Chadab 1979, 1980; Chadab-Crepet & Rettenmeyer 1982) and many ant species (Mirenda *et al.* 1980; LaMon & Topoff 1981; Droual 1983; pers. obs.) exhibit rapid evacuation or defensive responses. In order to have evolved these defensive responses to army ants, the ants and the associated birds and parasitic flies must exert a selective force on these prey species. However, it is difficult to estimate the actual impact of *E. burchelli* raids on the arthropod community. At Barro Colorado Island, Panama, each point in the forest is raided on average only once every 630 days by that species (Franks 1982a)—a rate too infrequent to be easily quantified by direct observation. For social insects that live in sedentary nests and recover slowly after being raided, the impact of army ant raids can be more easily assessed. Franks (1982b) and Franks and Bossert (1983) indicated that army ants significantly alter their prey species by keeping populations below saturation density. For nonsocial and less sedentary prey such as cockroaches and crickets, the impact of army ant foraging is more difficult to estimate. Absolute abundance of these organisms is reduced by approximately 50 percent immediately following the passage of an ant swarm, but immigration from nearby areas rapidly restores prey densities (Franks 1982a). Nevertheless, such predation certainly lowers the overall abundance of these organisms, and parasitization by flies must have an additional impact which is very difficult to quantify. In order to further evaluate the foraging of army ants and their impact on their prey species, we need quantitative data to support the estimated importance of predation by army ants, birds, and parasitic flies that is presented in Figure 3. Additionally, population studies of selected prey species may help to assess the long-term impact of army ant raids on the nonsocial arthropods inhabiting the forest-floor leaf litter.

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APPENDIX 1. Complete list of arthropods collected from the six paired leaf-litter plots before (B) and after (A) passage of a foraging swarm of *E. burchelli* army ants.^a

	1		2		3		4		5		6		Total
	B	A	B	A	B	A	B	A	B	A	B	A	
Onycophora	0	0	1	0	0	0	0	0	0	0	0	0	1
Argasidae	0	0	0	0	0	0	1	0	0	0	0	0	1
Acarina	0	0	0	0	7	2	6	3	1	2	3	0	24
Araneida	5	4	14	14	7	15	15	4	15	8	17	15	133
Chelonethida	4	1	7	0	17	1	6	0	5	0	6	7	54
Isopoda	2	1	3	2	15	15	15	0	15	15	22	3	108
Chilopoda	1	0	0	1	3	0	1	1	0	0	2	3	12
Diplopoda	2	0	2	0	4	2	2	0	0	0	11	4	27
Scolopendromorpha	0	0	0	0	0	0	0	0	0	0	0	2	2
Collembola	0	0	0	0	0	1	0	0	0	0	0	0	1
Thysanura	0	0	0	0	0	0	1	0	0	0	0	0	1
Dermaptera	0	1	1	0	1	0	1	0	0	1	1	0	6
Psocoptera	0	0	0	0	0	0	0	0	0	0	0	1	1
Orthoptera (total)	7	1	7	5	14	3	2	2	10	1	15	19	86
Acrididae	1	0	0	0	0	1	0	0	0	0	0	1	3
Gryllidae	0	1	0	2	1	0	0	0	2	0	3	0	9
Tetrigidae	0	0	0	0	0	0	0	0	0	0	1	0	1
Mantidae	0	0	0	0	1	0	0	0	0	0	0	0	1
Blattidae	6	0	7	3	12	2	2	2	4	1	11	18	68
Blattidae (sm. nymphs?)	0	0	0	0	0	0	0	0	4	0	0	0	4
Isoptera	0	1	0	0	0	0	0	0	0	0	0	0	1
Hemiptera (total)	0	0	0	1	0	0	1	0	0	0	3	2	7
Anthocoridae	0	0	0	0	0	0	0	0	0	0	0	1	1
Cydnidae	0	0	0	0	0	0	0	0	0	0	1	0	1
Reduviidae	0	0	0	1	0	0	1	0	0	0	1	0	3
Hemiptera (misc.)	0	0	0	0	0	0	0	0	0	0	1	1	2
Neuroptera													
Myrmeleontidae larva	0	1	0	0	0	0	0	0	0	0	0	0	1
Coleoptera (total)	1	0	10	0	3	3	8	1	10	6	11	13	66
Anthicidae	0	0	1	0	0	0	0	0	0	0	0	3	4
Tenebrionidae	0	0	0	0	0	0	0	0	0	1	0	0	1
Bostrichidae	0	0	0	0	0	0	4	0	0	0	0	0	4
Staphylinidae	0	0	3	0	0	0	2	0	2	0	4	4	15
Carabidae	1	0	2	0	1	0	1	0	1	0	0	1	7
Haliplidae	0	0	0	0	0	0	0	0	0	0	0	1	1
Nitidulidae	0	0	0	0	0	2	0	0	1	3	0	0	6
Chrysomelidae	0	0	0	0	0	0	0	0	0	0	1	1	2
Erotylidae	0	0	0	0	0	1	0	0	2	0	0	0	3
Ptinidae	0	0	0	0	0	0	0	0	0	0	1	0	1
Curculionidae	0	0	1	0	2	0	0	0	1	2	1	1	8
Histeridae	0	0	0	0	0	0	0	0	1	0	0	0	1
Scarabaeidae	0	0	0	0	0	0	0	0	1	0	0	0	1
Beetle larvae	0	0	3	0	0	0	1	0	1	0	3	1	9
Coleoptera (misc.)	0	0	0	0	0	0	0	1	0	0	1	1	3
Lepidoptera (total)	0	0	1	1	1	0	0	0	1	1	1	1	7
Adult	0	0	1	0	0	0	0	0	0	0	1	1	3
Larvae	0	0	0	1	1	0	0	0	1	1	0	0	4
Diptera (total)	0	0	0	0	0	2	2	0	0	0	1	4	9
Nematocera	0	0	0	0	0	0	0	0	0	0	0	2	2
Cyclorhapha	0	0	0	0	0	0	0	0	0	0	0	1	1
Drosophilidae	0	0	0	0	0	0	1	0	0	0	0	1	2
Larvae	0	0	0	0	0	2	0	0	0	0	0	0	2
Diptera (misc.)	0	0	0	0	0	0	1	0	0	0	1	0	2
													548

^a Hymenoptera: Formicidae were present in all samples but not counted.