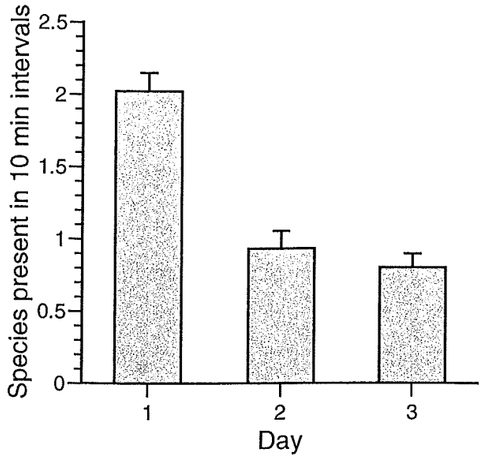

FIG. 4. The average number of species present per 10 min interval at a fruiting *Ficus lapathifolia* over 3 days (+ SE).

ample, when a population of trees fruits synchronously, such as during an oak mast, resources may be so overabundant that there is no selection for partitioning the resource and, therefore, no patterns in time or space would exist. With smaller, more ephemeral resources, like carrion, there might be a tendency for well-developed dominance hierarchies, with some species being efficient at locating unexploited resources and others being effective at dominating resource patches already occupied by the species. It seems possible that the extent and type of community structure varies with the size, quality, longevity and predictability of resources. As communities become more structured, it seems likely that overall resource use efficiency increases, thus permitting the coexistence of a more diverse assemblage of species.

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APPENDIX. Vertebrate foraging at a fruiting fig tree *(Ficus lapathifola)* in Corcovado National Park on 1 - 3 Februrary, 2002.

Common name	Scientific name
Agouti	*Dasyprocta punctata*
Common Black-hawk	*Buteogallus anthracinus*
Geoffroy' s Spider Monkey	*Ateles geoffroyi*
Crested Guan	*Penelope purpurascens*
Jaguarundi	*Herpailurus yaguarondi*
Little Tinamou	*Crypturellus soui*
Mantled Howler Monkey	*Alouatta palliata*
Red Brocket Deer	*Mazama americana*
Scarlet Macaw	*Ara macao*
Squirrel Monkey	*Saimiri oerstedii*
White-nosed Coati	*Nasua narica*
White-tipped Dove	*Leptotila verreauxi*

The Great Escape: Patterns in Arthropod Response to Army Ants

Matthew T. Burke, Jennifer L. Butcher, Lindsay V. Reynolds and Richard W. Hofstetter

Abstract: The army ant, *Eciton burchelli*, is a ubiquitous and apparently formidable predator of invertebrates and small vertebrates in Neotropical forests. We investigated the response of various arthropod taxa to army ants in both experimental and natural conditions. We hypothesized that arthropods would exhibit specific flight or fight defensive behaviors in response to army ants. Physical contact, rather than a volatile, is apparently the primary cue used to detect army ants, except in hymenopterans, some of which appeared to respond to army ant volatiles. When confronted with an advancing army ant swarm, 67% of 42 arthropods exhibited a "flee and freeze" behavior after physical contact with the ants. It seems probable that army ants have been a meaningful force in the evolution of arthropod behaviors, but that patterns of adaptations have also been influenced by limitations of sensory apparati and tradeoffs between escaping army ants and falling prey to associated antbirds.

Key Words: chemical cues, chemical receptors, defense, Eciton burchelli, *insects, pheromones*

Introduction

Army ants are among the primary predators of invertebrates in the Neotropics (Holldobler and Wilson 1990). Therefore, they may serve as an important selective force for arthropods upon which they prey. For example, selection should favor the development of behavioral or sensory systems that increase survival probabilities in the presence of a foraging swarm. Studies of social wasps indicate behaviors that are apparently the result of selective pressure from ant predation (Jeanne 1979). However, the cues that trigger these capture avoidance behaviors in wasps remain unknown and evolutionary responses of other invertebrates to army ants are even less understood.

Army ants lack vision and thus communicate and navigate using a variety of chemical pheromones. Army ants appear to have particular pheromones for different behaviors: attacking, defensive, raiding, colony recognition and bivouacing (Rettenmeyer 1983). Volatiles associated with army ant raids might be used by invertebrates to elicit escape behaviors. We hypothesized that arthropods would exhibit fight or flight escape behavior in the presence of predatory ants. We predicted that such behavior by the arthropods would be driven by their detection of army ant pheromones and tested this hypothesis in three experiments: arena trials, ant introduction to wasps nests *in situ* and direct observations at the head of a foraging army ant swarm.

Methods

Research was conducted on 2 - 4 February 2002 at the Sirena Biological Station, Corcovado National Park, Costa Rica. The arena trial was conducted on station premises, wasp trials were conducted at the station and on the Espavales Trail, and swarm observations were made 300 m west of the Los Patos Trail ~500 m north of the station.

Arthropod Arena

Volatiles associated with army ants were tested for their ability to elicit a behavioral response in arthropods. Leaf-cutter ants, which also employ complex pheromone systems, were used as a control. Various arthropods were collected from the field and forest edge near the Station. Arthropods were

identified to order (Table 1) and placed into the arena (a 60 x 30 x 10 cm plastic Tupperware container). Army ants were collected from the front of a raiding column on the Espavales trail 100 m SW of the station. Leaf-cutter ants were collected from a leaf-cutter column ~50 m from the Station. Approximately twenty individuals of each ant species were presented to target species within 10 x 10 cm^2 mesh bags in a random order. The arthropod's baseline behavior was observed for 2 min prior to the introduction of the ants. The bag of ants was then placed in the arena with the target arthropod, whose subsequent behavior (increased activity, moving away, jumping or no response) was recorded.

Hympenopteran Response

Using ants collected as above, we observed the responses of four different species (all order: Hymenoptera) to army ants and leaf-cutter ants. We tested 6 nests of *Polestes* sp. located on the underside of the roof of the Sirena Biological Station with 2 - 20 individuals per nest and three species on the Espavales Trail: a stingless bee nest (*Trigona fuluivelis*), a medium sized paper wasp nest (*Polybia* sp.) with approximately 20 individuals and a fourth wasp nest (unidentified species). Each nest was presented with seven stimuli: (1) empty mesh bag, (2) mesh bag with leaf-cutter ants, (3) mesh bag with army ants, (4) mesh bag with crushed leaf-cutter ants, (5) mesh bag with crushed army ants, (6) live leaf-cutter ants physically placed on the nest and (7) live army ants physically placed on the nest. Presentations were separated by at least 10 min to allow the wasps to return to baseline behavior (Jeanne 1979).

Natural Observations

To test the behavioral response of arthropods to the presence of an army ant swarm, we observed arthropods along the edge of an advancing *E. burchelli* swarm for 2 h. For each focal arthropod (observed until out of visual range or until the observers were forced to move away from the swarm), we recorded position relative to the swarm, and their behavior before and after (if applicable) making contact with individuals from the swarm.

Results

Arthropod Arena

For all but one species of arthropod, there was no change in behavior with the addition of confined army ants (Table 1), nor was there any apparent response to confined leaf-cutter ants.

Hymenopteran Response

Experimental introduction of ant volatiles to four hymenopteran species produced results ranging from no response to defensive posture (facing the ants, wings held erect), wing vibration and even physical removal of the ants (Table 2). Stingless bees (*Trigona fuluivelis*) increased flight activity and attack behavior towards the mesh bags when presented with both ant species. *Polybia* wasps responded to the physical presence of the ants but not to chemical cues. They displayed greater defensive behavior to army ants than leaf cutters, physically carrying the army ants off their nest while ignoring the leaf cutter ants. Placing ants on the nest caused an el-

TABLE 1. Strength of behavioral responses exhibited by seven arthropod taxa within small experimental arenas to army ants and leaf-cutter ants (control). Ants were presented in a mesh bag within 5 cm of the arthropod. Response was scored from 0 to ***, with 0 being no response and *** being a very strong response.

	army ants	leaf-cutter ants
Orthoptera spp.[a]	0	0
Hemiptera spp.[a]	0	0
Aracnidae spp.[b]	0	0
Lepidoptera spp.[a]	0	0
Coleoptera spp.[b]	*	0
Millipedia spp.[b]	0	0
Isopoda spp.[b]	0	0

[a]immature
[b]adult

TABLE 2. Strength of behavioral responses by four hymenoptera species in response to army ants and leaf-cutter ants (control). Ants were presented in a mesh bag within 5 cm of the nest. Response was scored from 0 to ***, 0 being no response and *** being a very strong response.

	Army ants in bag	Leaf-cutter ants in bag	Leaf with army ant scent	Leaf with leaf-cutter ant scent	Control bag	Control leaf	Army ants on nest	Control ants on nest
Polybia sp.	*	0	0	0	0	0	***	**
Trigona fuluivelis	*	*	*	*	0	0	***	**
Polestes sp.	*	0	0	0	0	0	**	**
Unid. vespidae	0	0	0	0	0	0	0	0

evated response in these wasps in which they displayed a sudden exodus of twenty individuals from the nest comb to cover the upper surface of the nest envelope, followed by wing-beating, defensive posturing and physically removing the ants from the nest. One day later, the entrance to the nest had been closed by approximately 50% (initial diameter ~6 cm). *Polestes* wasps exhibited only slight behavioral changes in response to army ant stimuli. There was no response to the control bag or to volatiles associated with either ant species. Placing ants on the nest caused the wasps to exhibit behaviors which included assuming a defensive position, wing beating, fleeing the nest and physically removing the ants. However, they had similar responses to both ant species with only a slight increase in their response to the army ants as opposed to the leaf-cutter ants.

Natural Observations

During six person-hours at the advancing head of an *E. burchelli* swarm, we recorded behaviors of 46 organisms representing 8 insect orders (Coleoptera, Dermoptera, Lepidoptera, Hemiptera, Homoptera, Hymenoptera, Orthoptera and Thysanoptera), Arachnidae and lizards (*Norops* sp.) (Table 3). Thirty-one (67%) individuals employed a "flee

TABLE 3. Number of individuals in various taxa exhibiting one of three types of behavior in response to an approaching army ant swarm.

	"Flee and freeze"	Flee on contact	Freeze
Lepidoptera[a]	2	--	--
Thysanoptera[b]	2	--	--
Coleoptera[b]	--	1	--
Hymenoptera[b]	1	4	--
Homoptera[b]	4	--	--
Orthoptera[b]	5	--	--
Hemiptera[b]	1	--	--
Dermaptera[b]	--	1	--
Aracnidae[b]	12	8	1
Reptilia[b]	4	--	--

[a]immature
[b]adult

and freeze" behavior, where they remained motionless until contacted by an army ant, at which time they moved a short distance (up to 5 cm) out of the column and froze again. This was repeated if further contact was made with the army ants. The "flee and freeze" behavior was exhibited by all the observed taxonomic groups except Coleoptera and Dermaptera. Fourteen individuals were motionless when we first detected them and then fled out of our sight without freezing after contact with the ants. Individuals of another ant species were observed fleeing in front of the advancing swarm, and contact was never made between the two ant species. None of the 46 animals that we watched were captured by army ants. Nor did we directly witness any other captures by army ants, although there was a steady stream of arthropod parts being carried by ants returning from the attack swarm.

Discussion

Non-hymenopteran arthropods did not respond to army ant volatiles (Table 1) but showed a strong response to physical contact with army ants (pers. obs.). There are several possible explanations for the lack of arthropod response to army ant pheromones. Notably, pheromones used by army ants to establish trails may be of high molecular weight and volatilize slowly, which would contribute to their effectiveness as trail markers and limit their detectibility by potential prey. It might also be that prey simply lack chemoreceptors that are a close enough match to army ant pheromones that natural selection can begin to act on them. In contrast, some wasps showed evidence of responding to army ant volatiles (Table 2). Wasps, being in the same order as ants, may more commonly have chemoreceptors, that by chance, can partially detect army ant pheromones; this could provide a starting point for natural selection to modify chemoreceptor systems for a new purpose (predator detection). This hypothesis of preadaptation in Hymenoptera is also consistent with our observations of an ant species that exhibited organized fleeing behavior before physical contact with the army ant swarm.

The "flee and freeze" behavior that was exhibited by many animals may be a compromise between fleeing army ants and escaping predation from the birds that often patrol the front of the swarm for escaping animals (Calvi et al. 2000, Dempsey et al. in this volume). Excessive movement by an arthropod may increase its chance of predation by birds, which are almost exclusively visual predators. One potential problem with this strategy is that army ants use CO_2 concentration gradients for prey detection (Holldobler and Wilson 1990). Thus, stationary insects would still be evident to army ants if they are respiring. Some arthropods have the ability to decrease their water loss by closing their spiracles (Brusca and Brusca, 1990). A byproduct of this adaptation is that CO_2 release is stopped for periods of minutes. It is possible that some invertebrates have co-opted this physiological capacity as a way to mask themselves to swarming ants. This could be tested with an infrared gas analyzer equipped to measure insect respiration. This hypothesis would also predict a tradeoff in the ability to flee, because high muscle activity could not be sustained in the absence of O_2.

One surprising result was that we did not witness a single capture at the front of the army ant swarm. We know there were captures occurring because of the prey parts being transported back to the bivouac (unpublished data from FSP 2002 field project). We hypothesize that the majority of prey captures occur at the center of the swarm where the army ants are more dense and more capable of overcoming prey. Many of these prey that succumb may be individuals that initially froze but were eventually surrounded by the swarm.

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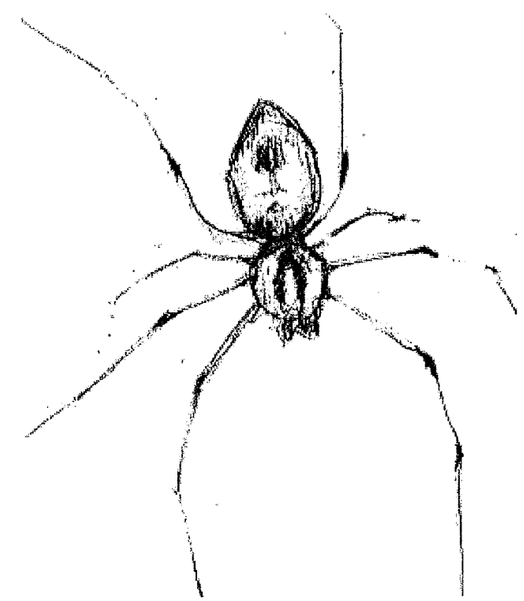
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