found only 17 species in common between the two habitats, we also found very few species in more than one replicate plot of the same habitat. Our sample size may not have been adequate to encounter enough individuals to determine the habitat restrictions of these morphospecies. Therefore, we have no evidence that the riparian habitat contains morphospecies not found in primary forest. Additionally, the diversity indices were similar between the habitats, indicating again that the species compositions of theplant communities were not very different.

In summary, the lack of morphospecies overlap between replicate plots makes it difficult to assess the contribution of the riparian habitat to the overall diversity of the primary forest. Additionally it is difficult to determine the effects of differing light levels between the riparian habitat and surrounding primary forest. Future studies directly comparing species in riparian areas to species in recently disturbed areas in primary forest would provide additional insight into the degree to which the riparian habitat contributes to the entire forest's diversity.

Table 1 (a-c). Characteristics of the riparian habitat (adjacent to and 1 m above the stream bed) and surrounding primary forest (5 m away and three meters above stream bed), along the north fork of the Quebrada Danta, Corcovado N.P., Costa Rica. *= significant difference.

	Riparian habitat	(SE)	Primary forest	(SE)	t	P
a) Soil Profile						
litter depth (cm)	5.63	(0.95)	6.50	(1.78)	-1.03	0.38
humic, leaf matter depth (cm)	1.75	(0.29)	2.75	(1.32	-1.36	0.27
b) Plant community structure						
woody 0-1m (ind/plot)	40.75	(6,10)	16.00	(3.58)	9.31	0.003*
woody 1-3m (ind/plot)	2.00	(1.41)	7.50	(2.10)	-2.02	0.14
woody basal area (cm^2/m^2)	29.85	(28.37)	95.13	(73.90)	-1.42	0.25
palm spp. (ind/plot)	2.75	(0.85)	1.00	(0.41)	2.05	0.13
musacious spp. (ind/plot)	0.75	(0.48)	1.25	(0.48)	0.78	0.50
fern (ind/plot)	.75	(0.48)	1.00	(0.41)	0.24	0.79
other herbaceous (ind/plot)	14.50	(6.29)	7.50	(4.71)	0.72	0.52
c) Species composition						
individuals/plot	66.50	(9.50)	42.75	(2.25)	2.07	0.13
morphospecies/plot	23.25	(2.25)	18.25	(2.17)	1.45	0.24
diversity (shannon index)/plot	2.38	(0.15)	2.32	(0.18)	0.35	0.75

FORAGING RECRUITMENT IN *ECITON* ARMY ANTS

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Abstract. Eciton army ants exhibit mass recruitment, with one ant laying a pheromone trail that attracts other ants. We hypothesized that as prey quantity increased, individual ants would recruit a greater number of sisters in less time. We found that recruitment does increase with prey quantity, though speed of recruitment does not. Our results imply that individual ants can distinguish different prey quantities, and this affects the way the colony forages.

INTRODUCTION

Army ants, *Eciton* spp., live in colonies of 30,000 to one million individuals and feed primarily on arthropods and other insects, including other ant colonies and social wasps (Janzen 1983). They exhibit a mass raiding behavior in which foraging workers are constantly branching outward along narrow odor trails in search of prey. This continuous foraging allows them to reduce the delay between prey encounter and recruitment. Once an ant finds suitable prey, the colony exhibits mass recruitment behavior. One ant is capable of recruiting one hundred ants in one minute (Chadab and Rettenmeyer 1975).

Both chemical and tactile communication are important to recruitment success. Ants drag their gasters to release a chemical trail from the raiding column to the prey. This trail alone contains the essential information for recruitment, but response is heightened by recruiter presence and tactile activity (Chadab and Rettenmeyer 1975).

The adaptive value of rapid mass recruitment has been shown in test raids of army ants on wasp nests by Chadab and Rettenmeyer (1975). They found that small numbers of ants were readily thrown off nests by wasps but that large numbers caused the adult wasps to abandon the nest and larvae. Therefore, it would be more efficient to recruit large numbers of ants rapidly to a large food source than to recruit either only sufficient numbers to transport prey or a preset number regardless of prey quantity.

Based on these findings and theoretical consideration, we hypothesized that army ants would recruit in proportion to the quantity of their prey: the more potential prey, the greater the number of ants that would be recruited to the site. Secondly, we hypothesized that they would recruit more quickly to larger quantities of prey compared to smaller quantities of prey.

METHODS

Our study was conducted in primary forest habitat near the Sendero Espavalles, Sirena Biological Station, Corcovado National Park, Costa Rica. We studied the first colony of army ants we encountered on 2 February 1995 at approximately 0700. We tentatively identified them as genus *Eciton* by the large mandibled soldiers. Due to their column foraging behavior, we believe they were *E. hamatum*.

To measure recruitment patterns, we had to find a suitable forage item that would induce ant recruitment. We did a preliminary test by placing centipedes, millipedes, leaf-cutter ants, and a cicada in the path of a foraging column. These items were ignored, except for minor interest in the leaf-cutter ants. We then noticed an abundance of large wasp larvae being carried by ants in the forage column. We removed a few of these larvae from the ants with tweezers and stored them in a clean vial. Upon larval replacement in the column, recruitment of ants was observed.

Using this information, we gathered approximately 50 larvae. We created 6-8 cm long "runways" from dead palm leaves on which we placed the larvae, following procedures of Chadab and Rettenmeyer (1975). Runways were then placed so one end was near but not in the foraging column. We performed 6 trials of two separate

treatments for a total of 12 trials: six with one larva per runway, six with five larvae per runway. For each replicate we recorded the time from first discovery of the larvae (first direct contact by the ant) until removal of that larva. We also recorded the time at which each consecutive larva was removed from the runway. We stopped timing the five larvae trials when the last larva was removed. We also recorded the number of ants present at the time each larvae was removed. Trials were paired so that the one larva trials were run for the same amount of time as the five larvae trials.

To avoid residual pheromone and activity effects, we used new runways for each trial. The location of the runways were randomly placed along a 3 m section of the foraging column.

RESULTS

Quantitative

We found significantly more ants recruited in the five-larvae trial versus the one-larva trial ($t=-4.45$, $df=10$, $P=0.001$, Fig. 1). The one-larva trials did not significantly differ from the five-larvae trials in the number of ants recruited by the time the first larva was removed (one-larva trial $\bar{x}=10.5\pm6.8$ ants, five-larvae trial $\bar{x}=17.5\pm8.3$ ants, $t=-0.65$, $df=10$, $P=0.53$). We also found no significant difference in the amount of time to remove the first larva between the two trials (one larva trial $\bar{x}=16.5\pm8.7$ sec, five larvae trial $\bar{x}=22.3\pm8.9$ sec, $t=-0.47$, $df=10$, $P=0.65$). We found that as time increased in the five larvae trials, number of ants recruited increased exponentially. We found that the best curve fit occurred at $y=0.545x^{1.12}$ ($R^2=0.878$, $n=30$, Fig. 2).

Observations

We repeatedly observed ants dragging their gaster after encountering the forage item, presumably releasing recruitment pheromones. This behavior was observed mainly with the five-larvae treatments. Often in these treatments, the ant did not attempt to remove a larva before returning to the foraging column. In contrast, the first ants to encounter single prey items often began to carry the prey to the column themselves. We were not able to accurately track the discovering ant to observe tactile recruitment. Other observations supported pheromonal recruitment. Empty runways, previously used for five larvae trials, were quickly swarmed by ants when placed next to the trail. New, unused runways were ignored.

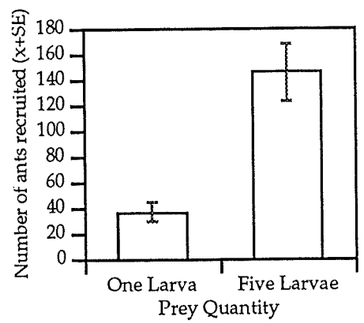

FIG. 1. Average number of ants recruited to two different quantities of prey (n=6 per treatment).

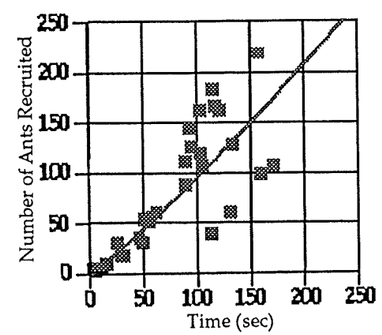

FIG. 2. Number of ants recruited for five larvae trials versus time.

Other typical army ant behaviors were observed. We saw multiple interlinked ant bridges up to 4 cm long, spanning gaps between branches and dead leaves. Group transport of prey, with three or more ants carrying one larvae, was also observed.

Shortly after the time that we believe the wasp nest containing the larvae was discovered by the ants, all of the foraging

columns in the area (five or more) became consolidated. Traffic increased along this combined column, until shortly after our trials were complete. Then the column dissolved, presumably because all the available larvae had been removed from the nest. We were not able to locate the central bivouac to see if another forage source had been discovered.

DISCUSSION

Our results support our first hypothesis that *Eciton* recruit in proportion to the quantity of prey discovered. However, our second hypothesis, that speed of recruitment would also vary with food quantity, was not supported. Thus, *Eciton* ants appear to be capable of laying a pheromone trail that varies in strength or length along the column depending upon prey quantity. This pheromone trial does not signal ants to be recruited at different speeds.

Because both treatments were run for the same amount of time, one potential difficulty with our methods is that the ants could stop responding to recruitment once the prey in the one-larva trial was depleted. However, the pheromone cues involved in this system are probably far more important than other factors, such as tactile cues (Chadab and Rettenmeyer 1975). Therefore, until the trail fades, the ants will continue to respond in the absence of a pheromonal cue to do otherwise. Since the ants swarm runways that were used in previous trials, we believe that there is no pheromonal cue which stops foraging behavior.

Our plot of recruitment versus time was found to have a best fit with an exponential function. This fit allows for several possibilities. One possibility, as Hölldobler and Wilson (1972) suggest, is that recruited ants would in turn recruit. A second possibility is that the number of ants recruited may be related to the length of the pheromone trail laid by the original ant. As the trail becomes longer along the column, more ants come in contact with it per unit time. Thus, more could be recruited per unit time. Further study could investigate which of these two possibilities is operating.

Our study indicates that individual ant behavior is more important in column foraging than previously believed. Further work exploring ant behavior at the individual level would be interesting and fruitful.

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