High rates of army ant raids in the Neotropics and implications for ant colony and community structure

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ABSTRACT

Army ants form nomadic insect colonies whose chief food is other social insects. Here we compare the rate of army ant raids with the average density of their potential prey from 28 New World subtropical and tropical localities. We estimate that army ant raids occur at the rate of 1.22 m^2 per day in tropical forests. Army ant raid rates increased with primary productivity, and with the density of potential prey (litter-nesting ant colonies), across sites. Our estimates of raid rates for army ant guilds are much higher than previously published estimates based solely on surface-raiding *Eciton*. Life-history theory predicts that high rates of predation on insect societies will select for both smaller average colony sizes and indeterminate colony growth, and these traits have been documented for tropical ant litter-nesting ants. Our results suggest that army ant predation can affect both patterns.

Keywords: ants, army ants, Ecitoninae, latitudinal gradient, life history, litter, predation, soil, tropics.

INTRODUCTION

Ants are important predators and herbivores in most terrestrial habitats (Hölldobler and Wilson, 1990). They reach their peak abundance in lowland tropical rainforests (Fittkau and Klinge, 1973; Kaspari *et al.*, 2000a). The high ant biomass in the tropics would appear to make them a conspicuous and attractive resource for predators and parasites. Although a long list of ants' natural enemies has accrued (Kistner, 1982), surprisingly little is known about the sources of mortality among mature ant colonies (Tschinkel, 1991; Kaspari, 2000).

Ants of the subfamily Ecitoninae – the army ants – have long been implicated as important predators of other ants (Wheeler, 1910). Army ant colonies are large (often with more than 100,000 adult workers) and nomadic, roaming the soils of the Neotropics and subtropics, overwhelming social insect colonies and harvesting their adults and brood (Jeanne, 1975; Rettenmeyer *et al.*, 1983; O'Donnell and Jeanne, 1990). The best-studied army ants

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are the swarm-raiders. Their raid fronts can extend several metres in width and travel hundreds of metres across the forest floor (Gotwald, 1982). Franks (Franks and Bossert, 1983; Franks, 1996) studied the raids of one swarm raider, *Eciton burchelli*, on a 1500 ha island in Panama. He suggested that army ant raids are cataclysmic but rare events in the forest litter, with (on average) only half of the forest floor contacted by *E. burchelli* raids every 240 days. However, a tropical rainforest may house a community of over 20 army ant species (Longino *et al.*, 2002). Many army ants raid in inconspicuous columns, and most species conduct their raids below the leaf litter or in the soil (Rettenmeyer *et al.*, 1983). Here we extend Franks' seminal work and show that army ant raids are surprisingly common events in tropical forest leaf litter. We found evidence that latitudinal gradients of army ant predation rates correspond with both primary productivity and litter ant colony density. We discuss the implications of our findings for the evolution of prey life-history traits and leaf litter community structure.

METHODS

We sampled army ant raid frequency as part of a larger project aimed at quantifying geographical patterns of ant diversity, body size and abundance in the New World (Kaspari *et al.*, 2000a,b, 2003; Kaspari, 2001). Here we focus on two regions where the Ecitoninae occur (Watkins, 1976, 1982, 1985): the North American subtropics (37–27°N latitude, 20 localities including desert and hardwood forest) and the New World tropics (< 27° N and S, eight tropical forests; see Kaspari *et al.*, 2000a, for a list of localities).

In each locality, a 330 m transect was randomly placed in relatively flat, undisturbed habitat. Thirty 1 m^2 plots were arrayed, 10 m apart, along the transect. The soil and litter in these plots was then searched for ant colonies. Each of the 30 plots at a locality was searched twice during daylight hours, ranging from 1 h after dawn to around sunset at each site (Kaspari *et al.*, 2000a). First the soil and litter were inspected for nests. In some cases, the plot was inspected for nests in the field, which took approximately 60 min. In other cases, a plot inspection took approximately 10 min (if there was no litter, or if litter was collected into plastic bags for inspection in the laboratory). After nest searches, plots were baited with crumbled pieces of shortbread cookie and surveyed for 30 min. We noted the ant colonies that recruited to these baits both from on and off the plot. We estimated total colony density of all ant species on a 1 m^2 plot as the average number of colonies located in the litter and soil. As ant colonies frequently have multiple nest entrances (Herbers, 1985), we counted each species no more than once per plot.

Plot inspections were sometimes interrupted by army ant raids arriving from off-plot or erupting from the soil. Raids covered most or all of each plot, and extended beyond the plots into neighbouring leaf litter. The army ant swarms and columns were observed and/or collected carrying prey; they were not observed carrying army ant brood. Therefore, we assumed that the swarms/columns represented foraging raids, rather than colony emigrations (Gotwald, 1982). Since the surveys were performed in a given amount of space and over a known amount of time, we were able to estimate the per-area rate of army ant raids. To do so we assumed that the surveys were random samples in time and space. For example, one *Neivamyrmex* sp. raid was recorded during sampling on Barro Colorado Island in Panama (Table 1). This translates into a 0.033 probability of encountering a raid column in one of the 30 plots. Given that each plot on Barro Colorado Island had an average sampling duration of 40 min, this yields an estimate of 0.05 raids per m^2 per hour.

Table 1. Army ant raid occurrence in 6 of 28 localities (8 tropical, 20 subtropical) that were sampled for litter ant density

Locality	Minutes observed per plot	Army ant species	Nature of activity
Tropical: Las Cruces, Costa Rica	90	*Labidus coecus*	4 columns
Tropical: La Selva, Costa Rica	90	*Labidus coecus*	2 columns
		Neivamyrmex balzani	1 column
		Eciton burchelli	1 swarm
Tropical: Monteverde, Costa Rica	90	*Labidus coecus*	2 columns
Tropical: Yasuni, Ecuador	90	*Labidus coecus*	1 column
		Labidus spininodis	2 columns
		Neivamyrmex sp. nov.?	1 column
		Eciton burchelli	1 swarm, 2 plots affected
Tropical: Barro Colorado Island, Panama	40	*Neivamyrmex* sp. nov.	1 column
Subtropical: Jornada LTER, New Mexico	40	*Neivamyrmex fallax*	1 column

Note: At each site we observed a transect of thirty 1 m^2 plots, 10 m apart. Unless otherwise noted, each raid (column or swarm) occurred on a different plot within a transect. 'Minutes observed per plot' depended on the amount of litter present and whether the litter was collected in plastic bags and returned to the laboratory, or analysed on site. Three tropical sites and 19 subtropical sites yielded no army ant activity on plots.

Multiplied by 24 h in a day, we estimate that on Barro Colorado Island there is an average of 1.2 raids per m^2 per day. We used this method to calculate the estimated raid rate for each subtropical and tropical site. From our litter surveys we were also able to estimate the density of litter nesting ant colonies at each site, and we previously estimated primary productivity (g C fixed$\cdot$m$^{-2}\cdot$year^{-1}; Kaspari *et al.*, 2000a,b). We tested for relationships between estimated army ant raid rates, litter ant colony densities and primary productivity among sites to identify ecological factors that could explain latitudinal differences in predation rates.

RESULTS AND DISCUSSION

Army ants are known to occur at each of the eight tropical sites that we sampled. We recorded 0–6 army ant raids from each tropical locality (Table 1). The raids, representing 1–4 species per locality, were recorded from different plots and all but two on different sample days. Summed across sites, an average m^2 plot in a tropical forest was estimated to experience 1.22 ± 1.1 (mean ± standard deviation; range 0–3.2) army ant raids per day. In contrast, only one of the 20 subtropical sites that ranged from desert to forest yielded an army ant raid. All of these sites were within the described geographic ranges of army ant species, and in habitats where they are known to occur (Watkins, 1985). Summed across the

subtropical sites, this resulted in an estimated raid rate of 0.06 ± 0.30 raids per m^2 per day (approximately one raid every 17 days).

   We estimated an individual litter ant colony's likelihood of being encountered by an army ant raid by taking the ratio of average raid rate to average colony density. The average density in the tropical localities (4.06 ± 1.3 colonies per m^2) is 4.9 times higher than in the subtropics (0.84 ± 0.68 colonies per m^2). The high density of tropical colonies is due, in part, to their small size (Kaspari and Vargo, 1995), with colonies of often fewer than 100 workers living in a small piece of twig (Kaspari, 1996b). Despite the greater overall colony density in the tropics, the estimated per-colony raid rate for litter-nesting ants is nonetheless 4.2 times higher in the tropics (0.299 raids per colony per day) than the subtropics (0.072 raids per colony per day). As we have noted previously (Kaspari et al., 2000a,b), primary productivity (NAP) accounted for much of the variation in litter ant colony density (Fig. 1; for the sites included in this study, linear regression $R^2 = 0.80$, $P < 0.0001$). Density of litter ant colonies and primary productivity were independently positively associated with army ant raid rate (Fig. 1; multiple linear regression, type III sums of squares significance test when predictor variable was entered last in the model: litter ant density, $F_{1,25} = 8.83$, $P < 0.005$; NAP, $F_{1,25} = 4.62$, $P < 0.05$).

   Earlier studies of the surface-raiding *Eciton burchelli* suggested that a point in space had a 50% chance of being raided every 240 days (Franks and Bossert, 1983). Our estimate of 1.22 raids per m^2 per day by a Neotropical army ant assemblage appears high in comparison. However, such an assemblage may include over 20 species (Rettenmeyer et al., 1983), many of which are more abundant than *Eciton burchelli* (Kaspari, 1996a). Most of these species are inconspicuous, raiding below the litter and often below ground (Perfecto, 1992; Berghoff et al., 2002). Our cleared patches of litter were windows into this otherwise invisible world.
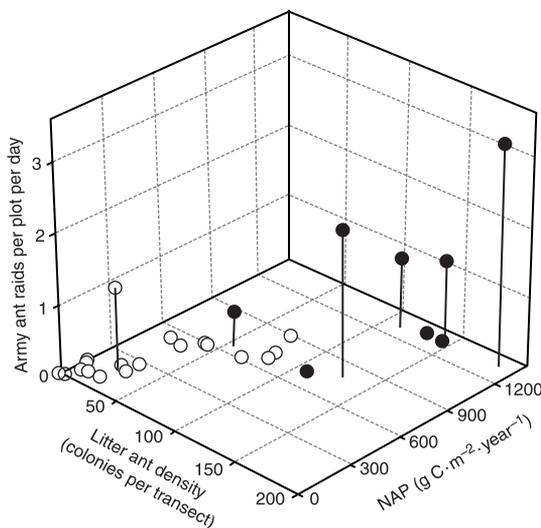
Fig. 1. Three-dimensional scatter plot showing relationship of estimated army ant raid rates with litter ant colony density and primary productivity (NAP) for 8 tropical sites (●) and 20 subtropical sites (○).

Our estimates of raid rates are provisional and come with a number of caveats. Two features of army ant biology suggest that our estimates of raid frequency are low. First, our methods could not detect below-ground raids (e.g. Perfecto, 1992). Furthermore, our assumption that raid rates were invariant over the daily 24 h cycle is probably not correct, as a large fraction of the army ant fauna raids primarily at night (Rettenmeyer, 1963). Estimates of raid frequencies do not necessarily translate into predation rates for litter-nesting ants. Our understanding of army ant diets is fragmentary, particularly for species of the genus *Neivamyrmex* which can account for half of the species richness in a Neotropical assemblage (Gotwald, 1982; Rettenmeyer *et al.*, 1983; Kaspari, 1996a). Therefore, ant species that nest in the leaf litter may not be at equal risk to army ant attack. Furthermore, army ants sometimes only crop colonies – harvesting to varying degrees pupae, reproductives and workers but missing (or sparing) the reproductive queen (Mirenda *et al.*, 1980; Franks and Bossert, 1983; Rettenmeyer *et al.*, 1983; Swartz, 1998; LaPolla *et al.*, 2002). Prey species may also vary in their effectiveness at defending against or fleeing from army ants. For example, litter-nesting *Aphaenogaster areonoides* climb nearby vegetation during raids (R. Dunn, personal communication). Thus the presence of a raid column in a plot does not necessarily mean that each colony in that plot is at equal risk of detection and death.

It has long been speculated that per-capita predation rates may generally be higher towards the tropics (Pianka, 1966), but few studies have documented this trend (Jeanne, 1979; Menge and Lubchenco, 1981; Sih *et al.*, 1985). Our results suggest that higher prey colony densities and high primary productivity interact synergistically to support elevated army ant predation pressure in tropical habitats. Even if our raid rate estimates are only roughly accurate, the conclusion that an ant colony is at higher exposure to army ant raids in the tropics seems robust. It has two implications worth further exploration. First, some life-history phenomena from tropical litter ant communities can be viewed as adaptations to life in a high-predation environment. Tropical ant species have colonies that average ten-fold fewer workers than those in the temperate zone (Kaspari and Vargo, 1995). Furthermore, most litter ant colonies sampled in an earlier study appeared to be growing as fast when they were small as when they were at their maximum observed size (Kaspari and Byrne, 1995; Kaspari, 1996b). Both traits are consistent with life-history models that predict adaptive responses when predation risk is high and constant over an individual's (or colony's) lifetime (Kozlowski, 1992).

Second, our results have implications for the structure of tropical ant communities. The swarm raider *Eciton burchelli* preys on large ant species that may behaviourally dominate the ants of the forest floor (Franks, 1996). *Eciton burchelli* raids can release resources for behavioural subdominants, with half the tropical forest floor in 'succession' from this episodic mortality (Franks and Bossert, 1983). Our results summarize the activity of a forest's army ant guild, and depict a steady and high raid rate (see also Berghoff *et al.*, 2002). Data on the diet and lethality of individual army ant species – many of which are known only from reproductives (Watkins, 1976) – are required to better understand how this constant activity impacts the more than 100 species of prey ants that occupy 1 ha of Neotropical forest floor (Cover *et al.*, 1990; Kaspari *et al.*, 2003).

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