Predation and patchiness in the tropical litter: do swarm-raiding army ants skim the cream or drain the bottle?

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Summary

1. Swarm-raiding army ants have long been considered as episodic, catastrophic agents of disturbance in the tropical litter, but few quantitative data exist on their diets, preferences, and, critically, their ability to deplete prey.

2. Here, we provide such data for two common species of swarm raiders broadly sympatric throughout the Neotropics: the iconic Eciton burchellii and the more secretive, less studied Labidus praedator. In Ecuador, Costa Rica, Venezuela and Panama, patches of forest floor were sampled for litter invertebrates immediately before and after army ant raids. These invertebrates have been shown to regulate decomposition and vary 100-fold in local densities across the forest floor.

3. Contrary to Eciton’s popular image, only Labidus consistently reduced the biomass of litter invertebrates and only then by an average of 25%. Eciton’s impacts were concentrated on rich patches of invertebrates, while Labidus prey depletion showed no such density dependence. Labidus reduced the biomass of some invertebrates—isopods, larviforms and coleoptera—by up to 75%; Eciton showed no such prey preferences.

4. Our results suggest that Eciton specializes on high biomass patches, while Labidus feeds profitably from any litter patch. Combined, these swarm raiders sum to be chronic, but not catastrophic, predators of common litter invertebrates of the brown food web.

Key-words: brown food webs, density dependence, invertebrates, predation, prey choice, tropical rainforest

Introduction

Army ants are group predators of the tropics. Most army ant species snake inconspicuously through the litter and soil, overwhelming and consuming colonies of other ants (Franks & Bossert 1983; Rettenmeyer et al. 1983; Powell & Clark 2004; Powell & Franks 2006; O’Donnell et al. 2007).

A small dark-coloured ant sometimes migrates in countless numbers. One day, at Bahia, my attention was drawn by observing many spiders, cockroaches, and other insects, and some lizards, rushing in the greatest agitation across a bare piece of ground. A little way behind, every stalk and leaf was blackened by a small ant. The swarm having crossed the bare space, divided itself and descended an old wall. By this means, many insects were fairly enclosed, and the efforts which the poor little creatures made to extricate themselves from such a death were wonderful. (Darwin 1839)
can be widespread. Ecton burchellii and Labidus praedator (henceforth Ecton and Labidus), for example, co-occur through much of the Neotropics (Watkins 1985). Rettenmeyer (1963) posited that Labidus ‘likely kills almost all the arthropods killed by burchellii on the forest floor’ and that ‘the minor workers of praedator are especially numerous and much smaller than burchellii [and that] these tiny workers probably attack minute ants and possibly Collombola and mites’. He also noted the lack of quantitative diet to test these hypotheses.

Daily swarm raids begin from a central nest and coalesce to form raid fronts from a few metres to over ten metres in width. These fronts are so densely populated with foragers that they appear to move across the forest floor in a continuous blanket. Prey captured by the swarm is immediately hauled back to a ‘bivouac’ nest that is moved on a regular basis (Rettenmeyer et al. 1983; Vieira & Höfer 1994).

Army ants may provide a partial answer to one enduring mystery regarding tropical brown food webs (the microbes and invertebrates that transform soil nutrients and dead plant tissue into multiple trophic levels, minerals and CO2): their 10- to 100-fold patchiness (Levings & Windsor 1985; Kursar 1989; Lodge 1996; Ettema et al. 1998; Chen & Wise 1999; Moore et al. 2004; Kaspari et al. 2008). Explanations for this patchiness typically begin with the analyses of leaf litter quality (Cadisch & Giller 1997) and soil chemistry (Schou & Schaefer 1998; Mulder, Van Wijnen & Van Wezel 2005): the ‘bottom-up’ supply rates of carbon and nutrient that feed microbes (Hairson, Smith & Slobodkin 1960). Predators can also enhance or diminish patchiness, however, depending on their ability at finding and exploiting rich and poor patches (Holling 1973). Such top-down causes of patchiness are far less common, despite the abundance of predators in brown food webs (Sih et al. 1985; Wardle 2002; Schmitz 2010).

Are army ants the conspicuous exception? Just as starfish in the rocky intertidal may eat their way across a landscape (Paine & Levin 1981), Franks and co-authors have evoked models of disturbance, patchiness and recovery of ant populations given Ecton’s large spatial footprint and episodic raiding (Franks 1980, 1982; Franks & Bossert 1983). Here, we ask three questions: (i) do Ecton and Labidus raids significantly depress the abundance and biomass of nonant litter arthropods; (ii) do they selectively cull certain taxa?; and (iii) do swarms act in a density-dependent manner so as to enhance or suppress patchiness? Unlike earlier studies, we compare two swarm-raiding army ant species that differ markedly in the body size of their workers and thus potentially their raid impacts. Moreover, we focus on the common micro- and mesoarthropods that make up most of the invertebrate diversity and potentially regulate decomposition in the tropical litter (Moore et al. 2004).

Materials and methods

We studied Ecton and Labidus swarms in the wet seasons of four forests, two from Central America and two from South America, with the greatest emphasis at the two Central American sites. Barro Colorado Island Panama, a 1500-ha island of seasonal moist forest in the central part of the Panama Canal, was sampled July 2002 and 20 July through 9 September 2003. La Selva Biological Station, Costa Rica, a 1600-ha tropical wet forest in the Caribbean lowlands of Costa Rica, was sampled 11 June through 4 August 2003. Santa Maria Valley, Henri Pittier National Park, Venezuela, a mix of 45 y.o. secondary forest and partially abandoned shade coffee plantation on the northern slopes of the Coastal Cordillera, was studied 1 August to 2 September 2003. Tiputini Biodiversity Research Station, Ecuador, a 650-ha collection of seasonally flooded (varzea) and terre firme primary forest, was sampled between 25 September and 16 October 2003 (Appendix S1).

Raids were located through regular trail walks. Once a swarm front was located, the investigator estimated swarm width and then sampled litter invertebrates c. 5 m in front of the swarm to quantify prey density in the area the swarm was about to raid. Five 0.25 m2 polystyrene chloride (PVC) quadrats were dropped haphazardly, and all litter was quickly collected down to mineral soil, sifted through a 1 cm mesh in a Winkler eclector (Bestelmeyer et al. 2000), and the siftate sealed in a cotton cloth bag. This would take c. 5 min. After verifying that the swarm passed over the cleared ‘before’ samples, the investigator would circle behind the swarm and harvest 5 ‘after’ samples in a similar fashion, but nestling quadrats between the branched army ant columns in the swarm’s wake.

Within c. 1 h, invertebrates were extracted for 48 h from the litter samples. In Ecuador and Venezuela, siftate was placed in a 0.5 cm mesh bag and hung in a Winkler frame; in Panama and Costa Rica, siftate was placed flat in a berlese funnel (Bestelmeyer et al. 2000). In all cases, invertebrates were extracted into 95% EtOH and sorted in M.K.’s lab.

We assume the difference in invertebrate size, density and biomass between before and after plots for a given raid reflects prey depletion, although some volant forms may have escaped into the air. We classified all invertebrates except ants into 58 taxonomic groups that were then sized by length on the long axis (e.g. 0.1–0.5, 0.5–1.0... and thereafter into 1 mm bins). We excluded ants from analysis because the arrival of a swarm raid often resulted in a flood of ants escaping with brood in an evacuation response, inflating the number of free-roaming ants that are harvested in after plots. Invertebrate mass was calculated using the equation for litter invertebrates (Kaspari & Weiser 2007): Mass (mg) = 0.0257 × size (mm)^3.818, which accounted for 89% of the variation across all taxa sampled. We compared the length distributions of these prey with those of the worker ants from both Ecton and Labidus (see Appendix S2).

We used paired t-tests to evaluate the hypothesis that Ecton and Labidus after average length and reduce the density (number 0.25 m⁻²) and biomass (mg 0.25 m⁻²) for all invertebrates pooled. We used the average value of the five quadrats from before and after plots (i.e. quadrats were subsamples). Sampling was necessary because of the 100-fold variability in abundance and biomass that characterizes litter systems. We then used ancova on log10 biomass to test the hypotheses that the proportion of invertebrates in after plots was a constant proportion of those found in before plots and that Ecton and Labidus shaped biomass similarly.

Finally, we used paired t-tests to evaluate the hypothesis that Ecton and Labidus reduce the biomass of ten taxa (generally ordinal, but with one group ‘larviform’, that included larvae of dipterans, coleopterans, lepidopterans, as well as rarer forms like nematodes and annelids). These ten taxa were found in sufficient numbers across raids and within plots to provide reasonable statistical power.
Results

We quantified the effects of 20 Eciton raids (12 in Panama, 5 in Costa Rica, 2 in Venezuela and 1 in Ecuador) and 10 Labidus raids (six in Panama, two each in Costa Rica and Ecuador). We sorted and sized a total of 119,619 invertebrates from 300, 025 m² quadrats of litter.

Eciton swarm raids had a larger footprint than Labidus in two respects. First, the swarm fronts of Eciton raids were about twice as large as Labidus (mean 8 vs. 5 m, Kruskal–Wallis $X^2_{2.8} = 48, P < 0.03$). Second, the modal length of a Labidus worker was c. 40% shorter than one from Eciton (3-6 vs. 5-6 mm, $n = 601$, 2630; Fig. 1). Although both size distributions were right-skewed, 96% of Eciton workers were larger than a modal Labidus. Of the ten most common litter taxa, mean body length varied 8-fold. Some prey taxa (e.g. coleoptera, diplopods, and larviforms) also showed considerable size variation. Still, the modal size of both species was typically larger than the mean size of their prospective prey (only diplopoda averaged larger than the modal size of a Labidus worker).

Despite their smaller size, Labidus swarms had a greater impact on the density of litter invertebrates (Fig. 2). Using paired t-tests (which account for the 10-fold patchiness in invertebrate density across sampled raids), Eciton swarms had no consistent effect on the average size of invertebrates ($t_{1.19} = 0.58, P = 0.57$), invertebrate density ($t_{1.19} = -1.48, P = 0.16$), nor biomass ($t_{1.19} = -1.73, P = 0.10$). In contrast, Labidus swarms left behind invertebrates that were 16% smaller ($t_{1.19} = -2.52, P = 0.03$), 16% less numerous ($t_{1.19} = -2.39, P = 0.04$), with 25% less total biomass ($t_{1.19} = -3.22, P = 0.01$).

We next explored whether litter impacts were density dependent (i.e. did the magnitude of prey reduction depend on the prey’s initial density, Fig. 3). An ANCOVA, after accounting for the expected correlation between the log₁₀ invertebrate biomass before and after a given swarm ($P < 0.0001$), showed that Labidus depleted 22% more prey biomass than Eciton on average (least square means biomass in after plots: 213 vs. 275 mg 025 m², $F_{1, 29} = 4.4, P = 0.041$). A significant interaction ($F_{1, 29} = 4.2, P = 0.0498$, Fig. 3) revealed Eciton and Labidus depleted prey in different ways. Labidus swarms depleted a uniform fraction of ‘before’ biomass (ordinary least squares regression: after = 0.048 before$^{1.3}$, test of exponent = 1: $F_{1.18} = 1.26, P = 0.29$). In contrast, Eciton left a larger fraction of invertebrate biomass in poor patches and depleted proportionately more prey in rich patches (after = 0.06 before$^{0.66}$, test of exponent = 1: $F_{1.18} = 7.09, P = 0.016$). In sum, Labidus impacts on prey biomass were density independent, and Eciton impacts were positively density dependent; Labidus appeared the more effective predator when invertebrates were relatively scarce; this advantage disappeared in rich patches.

![Fig. 1.](image1.png) The size of swarm raiders and their potential prey. The black and grey histograms represent the distribution of worker size among Labidus praedator (black) and Eciton burchellii (grey). Triangles represent the mean size (1 ± SE) of the 10 most common invertebrate taxa in the Neotropical forest litter. Both lengths are along the organism’s long axis.

![Fig. 2.](image2.png) Impact of swarm raiding army ants on the litter invertebrates of four Neotropical forests. Trajectories represent the changes in average invertebrate length, density or biomass before and after raids by 20 Eciton burchellii and 10 Labidus praedator raids. Each point is the mean of 5: 025 m² plots. Insets are the mean % change in the dependent variable, and p value was generated by a paired t-test.
We next examined how the two swarm raiders changed the biomass of 10 common taxa using a total of 20 paired \( t \)-tests (Table 1). \textit{Eciton} swarms failed to deplete any of the ten invertebrate groups using \( P < 0.05 \) criteria. In contrast, \textit{Labidus} swarms significantly depleted three taxa. Immediately following \textit{Labidus} raids, we extracted 75% less isopod biomass, 49% less larviform (e.g. diptera, coleoptera and lepidoptera larvae) and 52% less coleoptera biomass.

**Discussion**

Traditionally, army ants have been categorized as either column raiders, with a specialized diet, or swarm raiders that take a broader spectrum of prey from the litter (Schneirla 1971). Swarm raids appear to be derived traits that have evolved multiple times within the Old World and New World army ants (Brady & Ward 2005; Kronauer \textit{et al.} 2007) including independent origins in \textit{E. burchellii} and \textit{L. praedator}. This gross convergence in behaviour masks, as we show here, substantive differences in diet and responses to litter patchiness.

Here, we show for the first time that \textit{Labidus}, a taxon with a smaller footprint in terms of body and swarm size, was more likely to deplete invertebrate prey biomass in the tropical litter (some taxa by up to 75%), while \textit{Eciton} did not. A plot of the prey density left behind against initial prey abundance (Fig. 3) suggests why: \textit{Eciton} was less effective at reducing prey number in low-density patches. \textit{Labidus}, in contrast, consistently reduced invertebrate densities regardless of starting density and depressed them more than \textit{Eciton} in all but the richest patches.

These differences in foraging behaviour between \textit{Labidus} and \textit{Eciton} may arise from two opportunities afforded by \textit{Labidus}'s smaller body size. First, the larger \textit{Eciton} foragers march over the leaf litter in loosely packed swarms that move relentlessly forward. \textit{Eciton} swarms resemble a loose 2-D net, allowing small prey to slip between (and hide within) the cracks. In contrast, the small size of \textit{Labidus} foragers allows them to move through the litter and to achieve a higher local forager density in the fractal-like litter matrix (Kaspari & Weiser 1999). In a \textit{Labidus} raid, the ground appears to seethe as foragers swing back and forth in waves (Rettenmeyer 1963). Prey that cannot fly away or crawl upwards on the thinnest of stems (Fig. 4) fall victim to this fine-meshed 3-D web.

It is important to note that some of the difference between our before and after plots must represent prey escape, not mortality, among the most mobile prey taxa (Fig. 4). Nevertheless, escape from swarm raiders in the tropical litter does not necessarily equate to absence of mortality. Invertebrates

**Table 1.** Paired \( t \)-tests analyse the effect of army ant raids by 20 \textit{Eciton burchellii} and 10 \textit{Labidus praedator} on the biomass of 10 common groups of litter invertebrates ordered from large to small body size. For each raid, means from 5 \( 0.25 \text{ m}^2 \) plots were sampled 5 m in front of and following the raid. \( P \)-values in bold are significant at \( P < 0.05 \).

<table>
<thead>
<tr>
<th>Prey taxa</th>
<th>( E. ) burchellii</th>
<th></th>
<th></th>
<th>( L. ) praedator</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>mg</td>
<td>% change</td>
<td>( t )</td>
<td>( pr &gt;</td>
<td>t</td>
<td>)</td>
<td>( n )</td>
<td>mg</td>
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<td>-1.5</td>
<td>0.146</td>
<td>10</td>
<td>48.3</td>
<td>-45</td>
<td>-0.8</td>
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<td>-1.0</td>
<td>0.328</td>
<td>9</td>
<td>4.3</td>
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<td>-3.5</td>
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<tr>
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<td>-5</td>
<td>-0.3</td>
<td>0.804</td>
<td>9</td>
<td>22.3</td>
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<td>-3.2</td>
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<td>0.066</td>
<td>8</td>
<td>9.9</td>
<td>-50</td>
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<td>0.061</td>
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<td>7.5</td>
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<td>9</td>
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<td>Collembo</td>
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<td>10</td>
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<td>Acari</td>
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<td>0.440</td>
<td>10</td>
<td>1.3</td>
<td>-1</td>
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\( n = \) sample size, mg = average biomass of prey/\( 0.25 \text{ m}^2 \) following the raid, \% change = percentage change in litter biomass as swarm passes over, \( t = \) \( t \)-statistic.
that attempt to fly above or outrun *Labidus* and *Eciton* swarms feed a variety of waiting avian (Willis & Oniki 1978; Wrege et al. 2005; Kumar & O’Donnell 2007) and invertebrate (Rettenmeyer 1961) predators and parasites. If these avian and invertebrate predators harvest a significant mass of prey relative to the army ants, as suggested by Franks and others (Franks 1996; Wrege et al. 2005), then we underestimate the net effects of raids on prey mortality for both army ant species.

*Eciton*’s higher colony-level energy demands (brought about by larger body size of their workers, Hou et al. 2010) may also force the raid to simply move on when prey densities are too low to be profitable. If *Eciton* does have a higher giving-up density (Kotler & Brown 1988), two predictions follow. First, *Eciton*’s swarm velocity should increase when it encounters a low-quality patch. Second, *Eciton* should be at a disadvantage to *Labidus* in lower productivity ecosystems. We have no data to evaluate the first prediction, but the manipulations of Franks et al. (1991) — in which packets of prey are dropped in front of swarms — would be an excellent means of testing it experimentally. Regarding the second prediction, while *Eciton* and *Labidus* are regionally sympatric throughout much of southern Central America and tropical South America (Watkins 1985), a variety of observers have recorded that high elevation and likely less productive tropical forests have less *Eciton* and more *Labidus* activity (J Lattke pers. obs., Longino pers. obs, O’Donnell et al. 2007 but see O’Donnell et al. 2010) In *The Ants*, Holldobler & Wilson (1990) ponder the diversity of army ants in a tropical forest, asking, ‘How do all those Amazonas coexist?’ Our data suggest that the swarm raiders specialize on patches that vary in invertebrate density.

Swarm raids have been modelled as episodic disturbance followed by prey recovery (Franks & Bossert 1983; Pickett & White 1985). In support of this model, our data suggest that for some prey (like isopods), local mortality may be severe and that the spatial extent of this depletion is twice as large for *Eciton* than *Labidus*. At the same time, however, recovery by larger litter invertebrates (laterally, from adjacent litter and perhaps vertically from refuges in the soil) is also likely rapid (Franks 1980). Furthermore, patches of Neotropical litter may be hit so frequently (once day$^{-1}$ m$^{-2}$ by variety of army ants, including the common and ubiquitous *Labidus cocceus*, Kaspari & O’Donnell 2003; O’Donnell et al. 2007) as to obscure the notion of recovery time between raids. Rather than an occasional catastrophe, we propose that the high frequency of raids, and the ability of many prey to hide and recolonize in the shifting litter environment, may best describe a model of chronic predation. By continually ‘skimming the cream’ and not episodically ‘draining the bottle’, army ants may have an enduring impact on prey life history, if not patchiness. Chronic predation can generate strong selection on vulnerable litter invertebrate populations (Feener 1987; Vermeij 1987; Kozlowski 1992), favouring, for example, clades with powerful chemical defences (Eisner et al. 1978; Saporito et al. 2007) and individuals that reproductively mature at a small size in a precarious environment (Kaspari 2005).

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**References**


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Supporting Information
Additional Supporting Information may be found in the online version of this article.

Appendix S1. Further site description.

Appendix S2. Quantifying the size distribution of Eciton and Labidus workers.

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