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

Michael Kaspari[1,2]*, Scott Powell[3]†, John Lattke[4] and Sean O'Donnell[5]

[1]*EEB Graduate Program, Department of Zoology, University of Oklahoma, Norman, OK 73019, USA;* [2]*Smithsonian Tropical Research Institute, Balboa, Republic of Panama;* [3]*School of Biological Sciences, University of Bristol, Woodland Road, Avon, Bristol BS8 1UG, UK;* [4]*Museo del Instituto de Zoología Agrícola, Universidad Central Venezuela, Apartado 4579, Maracay 2101-A, Venezuela; and* [5]*Animal Behaviour Program, Department of Psychology, Box 351525, University of Washington, Seattle, WA, USA*

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

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)

*Correspondence author. E-mail: mkaspari@ou.edu
†Present address: Department of Ecology and Evolutionary Biology, University of Arizona, P.O. Box 210088, Tucson, AZ 85721, USA.

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 but conspicuous exception is the swarm raiders, which harvest a wide variety of nonant litter invertebrates, in addition to ant prey (Rettenmeyer 1963; Franks 1982). Swarm-raiding species have long attracted the interest of tropical ecologists, in part for the carnage that appears to accompany them (Darwin 1839; Schneirla 1955; Hölldobler & Wilson 1990). Of the 20 or so army ants that may be found in a tropical forest (Rettenmeyer 1963; Schneirla 1971), only two or three may swarm raid, but these species

can be widespread. *Eciton burchellii* and *Labidus praedator* (henceforth *Eciton* 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 Collembola 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 CO_2): 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 (Scheu & Schaefer 1998; Mulder, Van Wijnen & Van Wezel 2005): the 'bottom-up' supply rates of carbon and nutrient that feed microbes (Hairston, 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 *Eciton's* large spatial footprint and episodic raiding (Franks 1980, 1982; Franks & Bossert 1983). Here, we ask three questions: (i) do *Eciton* 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 *Eciton* 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 m^2 polyvinyl 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) = $0·0257 \times$ size (mm)$^{2·438}$, 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 *Eciton* and *Labidus* (see Appendix S2).

We used paired *t*-tests to evaluate the hypothesis that *Eciton* and *Labidus* alter 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). Subsampling was necessary because of the 100-fold variability in abundance and biomass that characterizes litter systems. We then used ANCOVA on $\log_{10}$ 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 *Eciton* and *Labidus* shaped biomass similarly.

Finally, we used paired *t*-tests to evaluate the hypothesis that *Eciton* 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, 0·25 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 $X^2_{15,8}$ = 4·8, 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 log_{10} 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

Fig. 2. 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: 0·25 m² plots. Insets are the mean % change in the dependent variable, and p value was generated by a paired *t*-test.

in after plots: 213 vs. 275 mg 0·25 m⁻², $F_{1,\ 29}$ = 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$^{1·5}$, test of exponent = 1: $F_{1,8}$ = 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 = 6·06 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.
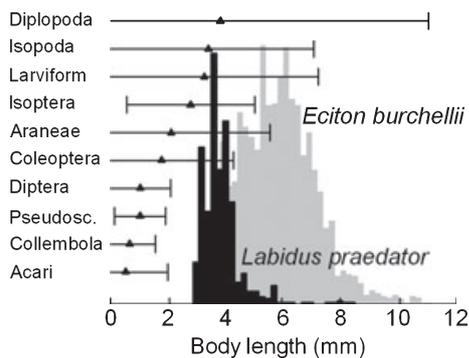

Fig. 1. The size of swarm raiders and their potential prey. The black and grey histograms represent the distribution of worker size among *Labidus praedator* (black) and *Eciton burchellii* (grey). Triangles represent the mean size (1 ± SE) of the 10 most common invertebrate taxa in the Neotropical forest litter. Both lengths are along the organism's long axis.
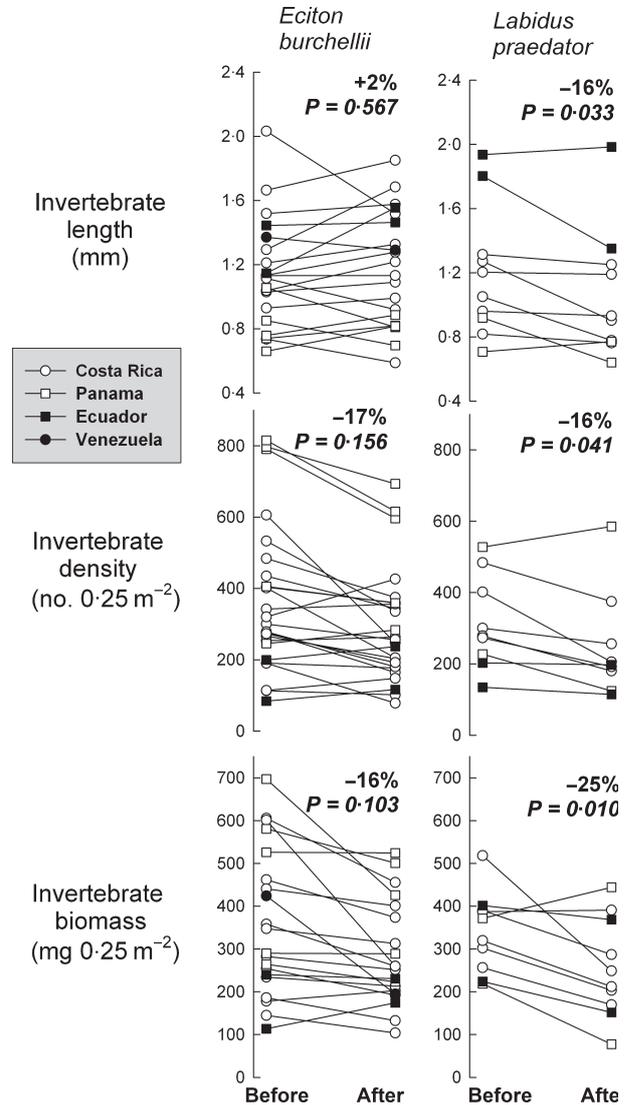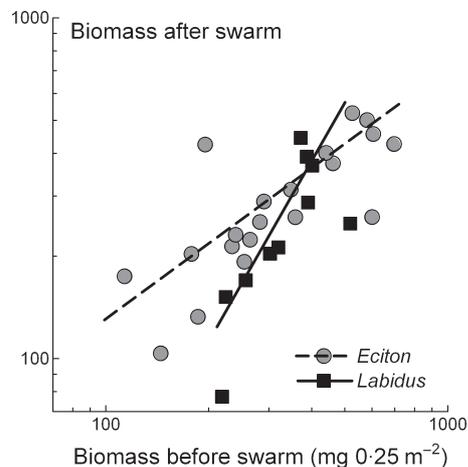
Fig. 3. Log_{10} biomass of invertebrates before and after army ant swarms. Each point represents a single raid. Lines are best fit by OLS regression for *Eciton burchellii* (dashed lines) and *Labidus praedator* (solid line); a significant interaction in slopes (see text) reveals that Eciton, but not Labidus, is less effective at reducing prey biomass in low biomass patches.

IMPACTS ON THE SIZE AND DENSITY OF 10 COMMON PREY TAXA

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). *Eciton* swarms failed to deplete any of the ten invertebrate groups using $P < 0.05$ criteria. In contrast, *Labidus* swarms significantly depleted three taxa. Immediately following *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 *et al.* 2007) including independent origins in *E. burchellii* and *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 *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 *Eciton* did not. A plot of the prey density left behind against initial prey abundance (Fig. 3) suggests why: *Eciton* was less effective at reducing prey number in low-density patches. *Labidus*, in contrast, consistently reduced invertebrate densities regardless of starting density and depressed them more than *Eciton* in all but the richest patches.

These differences in foraging behaviour between *Labidus* and *Eciton* may arise from twin opportunities afforded by *Labidus*'s smaller body size. First, the larger *Eciton* foragers march over the leaf litter in loosely packed swarms that move relentlessly forward. *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 *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 *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 *Eciton burchellii* and 10 *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 m^{-2} plots were sampled 5 m in front of and following the raid. *P*-values in bold are significant at $P < 0.05$.

Prey taxa	E. burchellii					L. praedator				
	n	mg	% change	*t*	pr > |*t*|	*n*	mg	% change	*t*	pr > |*t*|
Diplopoda	20	27·3	−30	−1·5	0·146	10	48·3	−45	−0·8	0·461
Isopoda	20	7·6	−11	−1·0	0·328	9	4·3	−75	−3·5	**0·007**
Larviform	19	16·5	−5	−0·3	0·804	9	22·3	−49	−3·2	**0·011**
Isoptera	11	6·5	−63	−2·1	0·066	8	9·9	−50	−1·2	0·236
Araneae	20	7·2	−79	−2·0	0·061	10	2·5	−56	−1·3	0·218
Coleoptera	20	5·3	−13	−0·7	0·506	10	7·5	−42	−2·5	**0·037**
Diptera	20	0·3	−14	−0·6	0·535	10	0·4	−27	−1·0	0·327
Pseudoscorp	20	0·3	−29	−1·4	0·176	9	0·3	−26	−1·9	0·085
Collembola	20	0·5	16	1·0	0·315	10	0·6	−55	−2·0	0·078
Acari	20	1·5	51	0·8	0·440	10	1·3	−1	−0·1	0·941

n = sample size, mg = average biomass of prey/0·25 m^2 following the raid, %-change = percentage change in litter biomass as swarm passes over, *t* = *t*-statistic.

Fig. 4. Isopods climb understory vegetation to escape a swarm raid of *Labidus praedator* in the tropical understory of Barro Colorado Island. Photo by Bob Holt.

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,* Hölldobler & Wilson (1990) ponder the diversity of army ants in a tropical forest, asking, 'How do all those Amazons 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 coecus*, 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).

Acknowledgements

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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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