

Army ants in four forests: geographic variation in raid rates and species composition

SEAN O'DONNELL*, JOHN LATTKE†, SCOTT POWELL‡ and MICHAEL KASPARIS§

*Animal Behavior Program, Department of Psychology, University of Washington, Seattle, WA, USA; †Museo del Instituto de Zoología Agrícola, Universidad Central Venezuela, Apartado 4579, Maracay 2101-A, Venezuela; ‡School of Biological Sciences, University of Bristol, Woodland Road, Bristol, Avon, BS8 1UG, UK; and §Department of Zoology, University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA

Summary

1. The New World army ants are top predators in the litter of tropical forest, but no comprehensive studies exist on variation in assemblage-wide activity and species composition. We used standardized protocols to estimate foraging raid rates and species composition of army ant communities in four Neotropical forests. The study sites spanned approximately 10° latitude, with two sites each in Central and South America.

2. We recorded a total of 22 species of army ants. The four sites varied in observed and estimated species richness. Species overlap was highest between the Central American sites, and lowest between the South American sites.

3. Raid activity varied significantly among sites. Raid activity per kilometre of trail walks was over four times higher at the most active site (Sta. Maria, Venezuela) than at the least active site (Barro Colorado Island, Panama). Furthermore, each site showed a different diel pattern of activity. For example, raid activity was higher during daylight hours in Costa Rica, and higher at night in Venezuela. Raid activity relationships with ambient temperature also varied significantly among sites.

4. The overall rate of army ant raids passing through 1 m² plots was 0.73 raids per day, but varied among sites, from 0 raids per day (Panama) to 1.2 raids per day (Venezuela).

5. Primarily subterranean species were significantly more abundant in Venezuela, and above-ground foragers that form large swarm fronts were least abundant in Panama. The site heterogeneity in species abundance and diel activity patterns has implications for army ant symbionts, including ant-following birds, and for the animals hunted by these top predators.

Key-words: ambient temperature, diel patterns, dominant species, Ecitoninae, foraging, species richness, top predator.

Journal of Animal Ecology (2007)

doi: 10.1111/j.1365-2656.2007.01221.x

Introduction

Predators often exert top-down effects on community structure, and these effects can permeate multiple trophic levels (Sih *et al.* 1985; Chapin *et al.* 1997; Pace *et al.*

1999; Terborgh *et al.* 2001). The species composition of guilds of consumers can influence ecosystem function, even in species-rich communities (Shiomoto *et al.* 1997; Pinnegar *et al.* 2000; Brose, Berlow and Martinez 2005; Schmitz 2006). An important but poorly studied question is how the species composition of guilds of top predators, and by extension their effects on community structure, vary geographically (Duffy 2002).

It is often assumed that predation pressure increases at lower latitudes (Estes 1995). Ants (Hymenoptera: Formicidae) are an exemplary taxon; predation by ants increases with decreasing latitude (Jeanne 1979), and

Correspondence: Sean O'Donnell, Department of Psychology, Box 351525, University of Washington, Seattle, WA 98195 USA. E-mail: sodonnel@u.washington.edu

Present address: Scott Powell, Universidade Federal de Uberlândia, Instituto de Biologia, Campus Umuarama Bloco 2D – sala 28, 38400-902 Uberlândia MG, Brazil.

ants play a major role as predators in tropical forests (Philpott and Armbrrecht 2006). Among ants, army ants stand out as important predators. Army ants use a unique type of foraging strategy, with the workers forming raids of thousands to millions of individuals that hunt in a highly organized and unified group. Workers in a raid cooperatively locate, subdue and harvest prey (Gotwald 1995). In the New World, army ants are represented by the subfamily Ecitoninae, which has five genera and more than 150 described species (Watkins 1976; Bolton 1995; Brady 2003). Most army ant species are restricted to tropical and subtropical latitudes (Watkins 1976).

Most of our knowledge about army ant biology comes from detailed studies of a few species, most notably *Eciton burchellii* (Westwood), at a single location in Central America (Barro Colorado Island, Panama; Rettenmeyer 1963; Schneirla 1971; Franks 1983). Data on army ant community structure and ecological impact are remarkably limited. In Neotropical lowland wet forest sites, however, the army ant community can comprise 20 or more sympatric species (Rettenmeyer *et al.* 1983; Quiroz-Robledo, Valenzuela-González and Suárez-Landa 2002). All army ants employ coordinated raiding behaviour (Brady 2003), but their diet, activity patterns and substrate use can differ dramatically (Franks 1983; Rettenmeyer *et al.* 1983; Powell and Franks 2006). Army ant diet specialization suggests that local variation in the relative and absolute abundance of army ant species will have strong effects on prey community dynamics.

The widespread species *E. burchellii* is considered a keystone predator in the leaf litter (Boswell, Britton and Franks 1998; Boswell, Franks and Britton 2000). *Eciton burchellii* raids leave significant decreases in the abundance and diversity of litter arthropods in their wake, and the raids promote diversity in the leaf litter ant community by creating a mosaic of patches in different stages of ecological succession (Franks and Bossert 1983; Otis *et al.* 1986). While data on the ecological impact of army ants are limited, the raids of the unstudied majority may have similar effects on their respective prey. The combined impact of the army ant community within tropical habitats is likely to be of major significance, but the magnitude and exact effects of these predators will depend on the diversity, activity and abundance of the army ant species present in any particular location. Army ant colonies also host a diverse array of symbionts, many of which may be host specific (Kistner 1982).

Army ants are abundant. By quantifying raids of all of the army ant species that visited leaf litter plots, Kaspari and O'Donnell (2003) showed that army ant raids occur at high densities in tropical forests, on the order of 1 raid m⁻² day⁻¹. Only a small proportion of this activity (17.6%) was contributed by *E. burchellii*. Many army ant species are nocturnal, partly or exclusively subterranean, or both (Rettenmeyer 1963; Schneirla 1971; Rettenmeyer *et al.* 1983). Army ant

activity is poorly measured using standard ant sampling protocols (Agosti *et al.* 2000).

The goal of this study was to quantify geographical variation in the species richness and abundance of army ants in the Neotropics. Our standardized sampling protocols were specifically designed to detect foraging army ants, and we collected data on above- and below-ground foraging (raid) activity by all army ant species we encountered (Berghoff *et al.* 2002; Kaspari and O'Donnell 2003; O'Donnell and Kumar 2006). We sampled in four Neotropical forests. The sites were chosen to span a wide latitudinal range (from approximately 0 to 10 N), and to represent both the Central American and the South American faunas. Army ant raid rates (summed across all species encountered) covary with local net primary productivity (Kaspari and O'Donnell 2003). It is not known if or how this broad pattern relates to changes in species richness, or in the relative abundance of different species. It is also unknown if army ant communities are uniformly affected by local environmental conditions. To address these questions, we tested for microclimate and time of day effects on army ant activity.

Materials and methods

SAMPLING SITES AND DATES OF DATA COLLECTION

All sites were sampled during the rainy season of 2003. Following is a brief outline of sampling dates and of the main habitat characteristics of the sites.

Barro Colorado Island Research Station, Panama (henceforth BCI); 9 09'N, 79 50'W; 20 July–9 September 2003. Elevation range was 60–190 m AMSL. BCI is a 1500-ha island in the central part of the Panama Canal. The island is completely forested, except for the small lab-clearing (Leigh 1999).

La Selva Biological Station, Costa Rica (henceforth La Selva); 10 26'N, 83 59'W; 11 June–4 August 2003. Elevation range was 40–130 m. La Selva is located in the Caribbean lowlands of northern Costa Rica, and comprises 1600 ha of tropical wet forests and disturbed lands (McDade *et al.* 1994).

Santa Maria Valley, Henri Pittier National Park, Venezuela (henceforth Sta. Maria); 10 22'N 67 49'W; 1 August–2 September 2003. Elevation range was 530–840 m.

Tiputini Biodiversity Station, Ecuador (henceforth Tiputini); 0 38'S, 76 08'W; 25 September–16 October 2003. Elevation range was 190–230 m. This site comprises extensive primary lowland forest adjacent to Yasuni National Park.

TRAIL WALKS

We chose trails to walk repeatedly for the purpose of sampling army ant raid activity at each site. Trails were located in primary forest, but some of the trails passed

through areas of old second growth forest (> 40 years regeneration). The trails ranged from 1.0 to 4.7 km in length. Total trail walk distances were, BCI: 66.4 km; La Selva: 63.1 km; Sta. Maria: 96.6 km; Tiputini: 42.6 km.

Walking trails is effective for detecting army ant activity for several reasons (Rettenmeyer 1963; Kaspari 1996; O'Donnell and Kumar 2006). First, surface army ant raids are often roughly linear, radiating out from the bivouac to maximum distances of 100 m or more (Rettenmeyer 1963; Schneirla 1971; Franks 1983). The raid columns are likely to intersect trails. Second, raids that cross-cleared trails are more likely to be detected than raids travelling through the litter, where they are obscured. Finally, the soil on trails is usually compacted, which forces subterranean army ants to travel above ground temporarily. It is not uncommon to see a column of army ants exit a hole or the deep litter layer on one side of a trail, cross the trail on the surface, and then return underground or into the deep litter immediately on the other side.

We searched for army ant activity while walking the surveyed trails at speeds of approximately 1 km h⁻¹. We conducted a maximum of two walks per site per calendar day. Walks began during four different time blocks. The range of start times for each block was: a.m. dark (01.58–04.55 h), a.m. daylight (08.02–10.30 h), p.m. daylight (12.28–15.37 h) and p.m. dark (19.15–20.16 h). At the start of every walk we noted which trail we were sampling, time to the nearest minute, air temperature (all temperatures were taken to the nearest 0.1 °C with a digital thermometer at 1.5 m above ground), and current weather conditions (sky: clear, partly cloudy or overcast). A small number of walks at each site (≤ 5 per site) were cancelled or shortened during periods of heavy rainfall. During trail walks we continually scanned the ground for army ant activity. We recorded time to the nearest minute, and we stopped for approximately 10 min to collect data and voucher specimens into 70% ethanol whenever we encountered army ants. At the end of each walk we noted time and air temperature.

We tested for relationships of sample site, time of day, and weather variables with the per-kilometre rate of army ant raid encounters using general linear models (GLM) implemented in SAS version 9.1 software. For post-hoc comparisons of means we used Tukey's Honestly Significant Difference (HSD) test, with critical alpha set at 0.05.

LITTER PLOT WATCHES

At three of the sites (excluding La Selva) we estimated army ant raid encounter rates per area per unit time. We observed 1 m² plots, cleared of leaf litter down to bare soil (Kaspari and O'Donnell 2003). The plots were arranged in transects from a randomly chosen starting point with each plot separated by 10 m. Sampling effort was as follows: (1) BCI: six transects,

19–20 plots each, 119 plots total; (2) Sta. Maria: 16 transects, 20 traps each, 320 plots total; (3) Tiputini: nine transects, 15 traps each, 135 plots total. All transects were located in primary forest. Plot watch data were collected during daylight hours, and transect set times were evenly divided between morning and afternoon starts at each site. All plots in each transect were visually inspected for army ant raid activity at 30-min intervals. We collected vouchers of army ants seen in the plots into 70% ethanol for species identification. Mean plot observation times were 2.25 h (Venezuela) or 3 h (BCI and Tiputini). We recorded how many plots were visited by army ants, and calculated raid rates m⁻² day⁻¹ for each site:

$$\frac{(\text{number plots with raids})}{(\text{number plots observed})} \bigg/ \frac{(\text{mean observation time per plot in hours})}{24 \text{ h}}$$

UNDERGROUND BAITED TRAPS

We placed baited pitfall traps at three of the sites (excluding La Selva) to sample underground army ant activity (Weissflog *et al.* 2000; Berghoff *et al.* 2002; O'Donnell and Kumar 2006). Sampling effort was as follows: (1) BCI: six transects, 15–21 traps each, 111 traps total; (2) Sta. Maria: 12 transects, 10 traps each, 120 traps total; (3) Tiputini: nine transects, 15 traps each, 135 traps total. We did not include traps that were destroyed by animals, or flooded, in our analyses. We baited the traps with oil expressed from canned tuna fish, or with peanut butter. The traps consisted of plastic cups, 13 cm tall and 8 cm in diameter, with a 3 cm diameter hole cut in the bottom. To place the traps, we dug a hole 15 cm deep with a bulb planter, baited the bottom of the trap, and inserted the trap into the hole. We covered the baited cup loosely with a larger inverted cup to allow access by ants, but prevent rainwater from entering. Transect set times were evenly divided between morning and afternoon starts at each site, and the traps were left in place for approximately 6 h before being checked for army ant activity. We collected vouchers of army ants found in the traps into 70% ethanol for species identification.

QUANTIFYING SPECIES RICHNESS

Species richness data were analysed using EstimateS software (R.K. Colwell: ESTIMATES 7.5, <http://viceroy.eeb.uconn.edu/EstimateS>). For species accumulation curves we plotted Mao Tau, the number of army ant species expected for a given number of encounters, calculated from the observations at each site (Colwell, Mao and Chang 2004). Extrapolations of species richness at each site were made using the Abundance-based Coverage Estimator (ACE; Chao *et al.* 2000). We used Chao's abundance-based Jaccard index to estimate the degree of species sharing among sites, or Beta-diversity patterns. For each pair of sites, the Chao–Jaccard index calculates the probability that two

randomly chosen raids, one from each of the sites, would both belong to a species shared among the two sites (Chao *et al.* 2005).

Results

TOTAL SPECIES RICHNESS

We recorded 22 species of army ants in total (Supplementary appendix 1). Thirteen species were observed at Sta. Maria, 10 each at La Selva and BCI, and nine at Tiputini. Most species were recorded during trail walks, while one species at one site was recorded only via underground bait sampling [*Neivamyrmex adnepos* (Wheeler) at BCI].

TRAIL WALK SPECIES RICHNESS AND BETA DIVERSITY

Species accumulation curves from the trail walk samples showed evidence of approaching asymptotes at each site, and suggested that species richness was highest at Sta. Maria (Fig. 1a). Extrapolations of trail

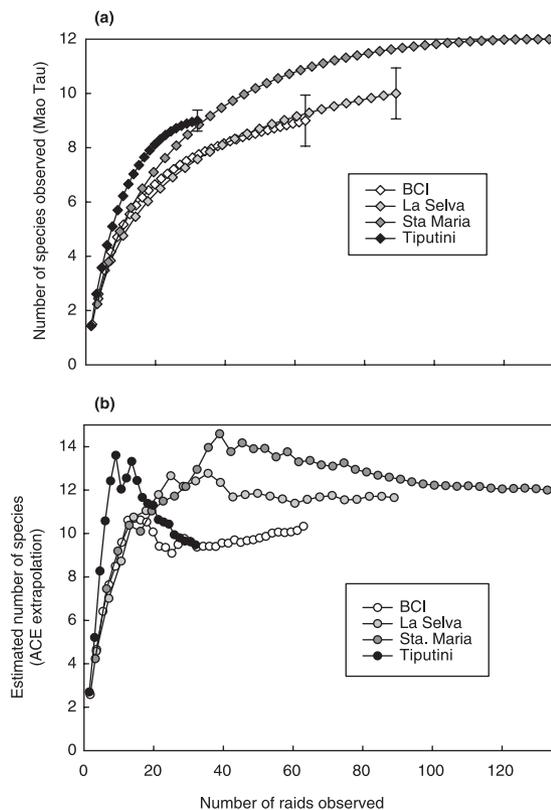


Fig. 1. (a) Cumulative expected number of species of foraging army ants encountered on trail walks (Mau Tau statistic) plotted against sampling effort (number of raids encountered) for four Neotropical forest sampling localities. The error bars on the final observation, which represents the number of raids seen at that site, are SE. (b) Cumulative extrapolated number of species of foraging army ants to be encountered on trail walks (Abundance Coverage Estimator statistic) plotted against sampling effort (number of raids encountered) for four Neotropical sampling localities.

walk species richness approached asymptotes at all sites, and suggested that no additional species were to be expected at Tiputini and Sta. Maria, while approximately two additional species could be expected at BCI and La Selva (Fig. 1b).

For trail walk raid encounters, the estimated rate of species sharing was highest between the two Central American sites (BCI and La Selva), and species sharing was lowest between the two South American sites (Sta. Maria and Tiputini; Table 1).

SITE, TIME, AND WEATHER RELATIONSHIPS WITH RAID RATES DURING TRAIL WALKS

The sites differed significantly in per-kilometre rates of raid encounters during trail walks (Fig. 2; multiple linear regression $F_{3,106} = 24.0$, $P < 0.001$). Per-kilometre raid encounter rates varied more than fourfold among sites, from a high of 2.14 raids km^{-1} at Sta. Maria to a low of 0.53 raids km^{-1} at BCI (Fig. 2). *Post-hoc* analysis showed that trail walk raid rates were higher at Sta. Maria than all other sites, and that the other sites did not differ.

The sites also differed in their daily patterns of raid activity (Fig. 2; multiple linear regression, site \times time block interaction term $F_{9,106} = 4.1$, $P < 0.0005$). At two sites, La Selva and Sta. Maria, raid activity varied significantly among time blocks (Fig. 2; Table 2). In both cases, *post-hoc* analysis showed that dark morning activity differed from light morning activity, but the patterns were in opposite directions. Dark morning raid activity was lower at La Selva and higher at Sta. Maria (Fig. 2).

The sites differed in air temperatures during trail walks (Fig. 2; multiple linear regression, $F_{3,103} = 65.4$, $P < 0.0001$), and *post-hoc* analysis showed that each site differed from all other sites. BCI was the warmest site (range of time block mean temperatures 26.2–27.2 °C), and Sta. Maria was the coolest (range of time block mean temperatures 21.8–24.8 °C). The sites did not differ in the pattern of temperature changes over the course of the day (Fig. 2; multiple linear regression, site \times time block interaction term $F_{9,103} = 0.85$, $P = 0.57$). The strongest temperature differences were typically between trail walks conducted at night vs. in the day (Fig. 2). Within sites, air temperatures differed significantly among time blocks except at BCI (Fig. 2; multiple linear regression, BCI: $F_{3,29} = 1.2$, $P = 0.37$; La Selva: $F_{3,19} = 9.1$, $P < 0.001$; Sta. Maria: $F_{3,32} = 8.1$, $P < 0.0005$; Tiputini: $F_{3,15} = 5.0$, $P < 0.05$). Trail walk raid rates were positively correlated with temperature at BCI ($n = 35$, $r = 0.39$, $P < 0.05$) and La Selva ($n = 25$, $r = 0.45$, $P < 0.05$), positively but not significantly related to temperature at Tiputini ($n = 21$, $r = 0.28$, $P = 0.22$), and negatively correlated with temperature at Sta. Maria ($n = 38$, $r = -0.33$, $P < 0.05$). After accounting for time block effects on temperature, raid rates varied significantly with ambient temperature only at BCI (Table 2). Sky conditions bore no significant relationships with trail walk raid rates at any site (Table 2).

Table 1. Observed and estimated rates of species-sharing (beta diversity) among sites for army ant raids encountered during trail walks. The highest and lowest Chao-Jaccard estimates of species sharing are indicated in **bold text**

Site 1 (no. of species observed)	Site 2 (no. of species observed)	No. of species shared	Chao est. no. of species shared	Chao-Jaccard abundance-based estimate
BCI (9)	La Selva (10)	7	7.57	0.96
BCI (9)	Sta. Maria (12)	7	8.15	0.54
BCI (9)	Tiputini (9)	5	6.14	0.64
La Selva (10)	Sta. Maria (12)	7	9.04	0.52
La Selva (10)	Tiputini (9)	4	4.00	0.51
Sta. Maria (12)	Tiputini (9)	4	4.00	0.38

Table 2. Results of multiple linear regression tests for relationships of time block and weather variables with army ant raid rates (raids per kilometre) sampled at four Neotropical sites. Significant relationships are shown in **bold type**

Site	Predictor variable	d.f. predictor, error	F statistic	P-value
BCI	Time block	3,28	1.04	0.39
	Air temperature	1,28	5.15	< 0.05
	Sky conditions	2,28	0.90	0.41
La Selva	Time block	3,18	4.90	< 0.05
	Air temperature	1,18	0.05	0.83
	Sky conditions	2,18	0.64	0.54
Sta. Maria	Time block	3,31	3.54	< 0.05
	Air temperature	1,31	0.13	0.72
	Sky conditions	2,31	1.35	0.27
Tiputini	Time block	3,14	0.44	0.73
	Air temperature	1,14	1.49	0.24
	Sky conditions	2,14	0.00	1.00

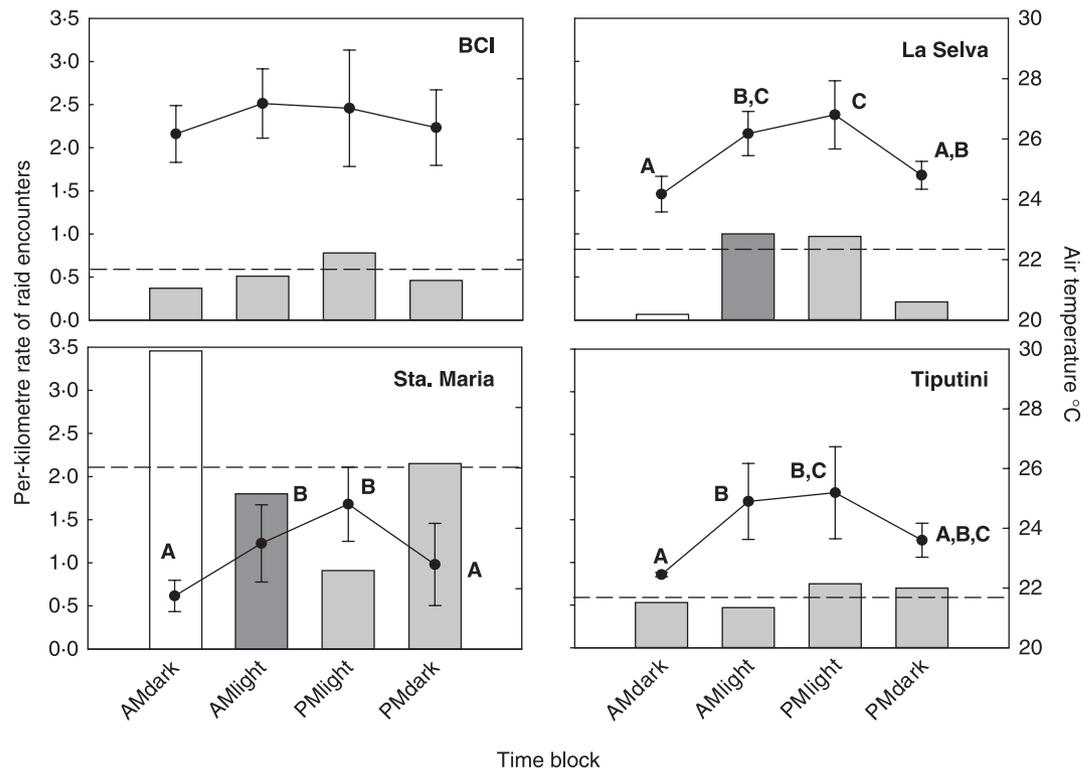


Fig. 2. Mean per-kilometre rates of encountering army ant raids (bar graph) at four different Neotropical forest sampling localities. For each site, each bar represents the mean rate of encounter during a single time block. Medium shading indicates raid rate means that did not differ among time blocks within sites; open and dark bars differed significantly only from each other, according to ANOVA *post-hoc* tests (Tukey HSD). The dashed horizontal line represents the overall mean site per-kilometre rate of raid encounters. Also plotted as a line graph are time block mean \pm SD air temperatures. Letters indicate temperature means that differed among time blocks within a site according to ANOVA *post-hoc* tests (Tukey HSD). All data are plotted on the same raid rate and temperature scales to facilitate direct comparisons among sites.

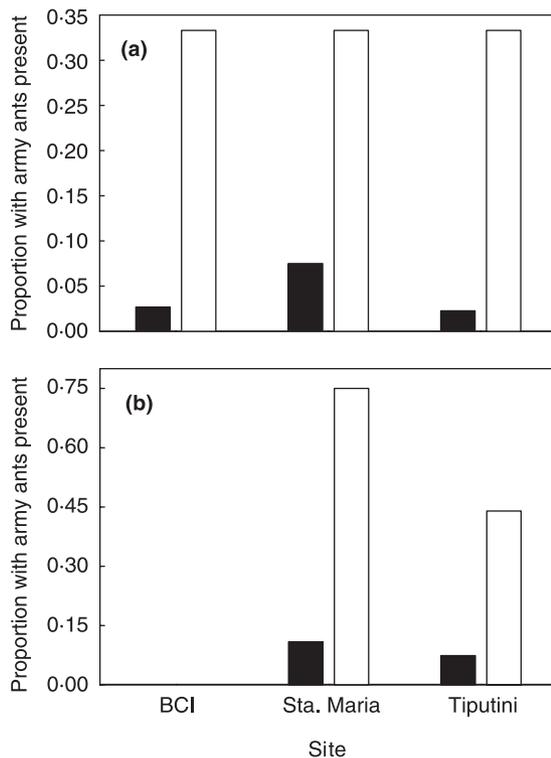


Fig. 3. (a) The proportion of underground bait traps (shaded bars) and bait trap transects (open bars) that were visited by army ants at three Neotropical forest sampling localities. (b) The proportion of cleared 1 m² plots on the soil surface (shaded bars) and plot transects (open bars) that were visited by army ants at three Neotropical forest sampling localities.

BAITED TRAPS

Baited underground traps attracted army ants at each of the three sites where they were used (Fig. 3a; Supplementary appendix 1). One-third of the bait trap transects were visited by army ant raids at each site. Pooled across transects, Sta. Maria had the highest per-trap rate of army ant encounters and Tiputini had the lowest (Fig. 3a). Two species were recorded in the bait traps at each of the three sites, and *Labidus coecus* (F. Smith) was recorded in bait traps at all sites (Supplementary appendix 1).

PLOT WATCHES

Plot watches at Sta. Maria recorded the highest rates of encounter at both the transect and plot levels, while no army ants were recorded during plot watches at BCI (Fig. 3b). The observed rates of army ant visitation to plots yielded estimates of 0 (BCI), 0.59 (Tiputini), and 1.16 (Sta. Maria) raids m⁻² day⁻¹, or 0.73 raids m⁻² day⁻¹ across all sites. Four species were observed in the plots at both Sta. Maria and Tiputini (Supplementary appendix 1).

DOMINANT SPECIES

To assess the importance of abundant species in explaining site differences in army ant raid rates, we

examined the activity patterns of the four species that were most frequently encountered during trail walks. These four species: *L. coecus*, *Eciton hamatum* (Fabricius), *Labidus praedator* (Latreille) and *E. burchellii*, represent 21% of the species observed on trail walks, but they accounted for most of the raid activity at each of the four sites: La Selva 70%, BCI 73%, Sta. Maria 62%, Tiputini 66%. Each of the most common species was observed at all four sites except *E. hamatum* at Sta. Maria, which is outside of this species' geographical range (Lattke, unpublished data). The other three sites did not differ in *E. hamatum* raid activity ($F_{2,56} = 0.06$, $P = 0.95$). The sites differed significantly in the relative per-kilometre activity rates of the other three species (Fig. 3B; *L. coecus*: $F_{3,87} = 11.4$, $P < 0.0001$; *L. praedator*: $F_{3,87} = 15.1$, $P < 0.0001$; *E. burchellii*: $F_{3,87} = 9.9$, $P < 0.0001$). *Post-hoc* comparisons suggested that *Labidus coecus* and *L. praedator*, both of which frequently forage underground, were most active at Sta. Maria, while the other sites did not differ. *Eciton burchellii* activity levels were highest at La Selva. While the other sites did not differ significantly, *E. burchellii* raid rates were lowest for BCI trail walks (Fig. 4).

Despite differences in overall raid activity, the behaviour of the four most common species was generally consistent among sites. Sites did not differ in trail walk raid rates across time blocks, temperature, or sky conditions for any of the four most common species (tested using multiple regression interaction terms, all $P > 0.25$). The only exception was a significant site \times time block interaction for *L. coecus* ($F_{9,87} = 2.00$, $P = 0.048$). This was largely explained by an exceptionally high a.m. dark encounter rate at Sta. Maria (mean = 1.24 encounters per km) relative to the same time block at the other sites (La Selva and Tiputini means = 0.0 encounters per km; BCI mean = 0.04 encounters per km).

Discussion

GEOGRAPHIC VARIATION IN SPECIES COMPOSITION AND DENSITY

Our data show that the species composition, and to some extent the species richness, of army ant guilds varies among lowland Neotropical sites. The number and identity of army ant species present at a given site, and their relative densities, may have dramatic implications for top-down effects on forest arthropod communities. Within a trophic level, consumer species often vary widely in their effects on prey communities (Paine 1992; Raffaelli and Hall 1996; Wootton 1997). Whether all army ant species exert similar effects on prey communities is unknown. The degree of functional overlap among army ant species as predators will depend in part on their diet breadth, prey preferences and predation rates. The few data sets on New World army ant prey choice suggest a high degree of specialization but prey records are unavailable for most army ant species and are particularly poor for those species

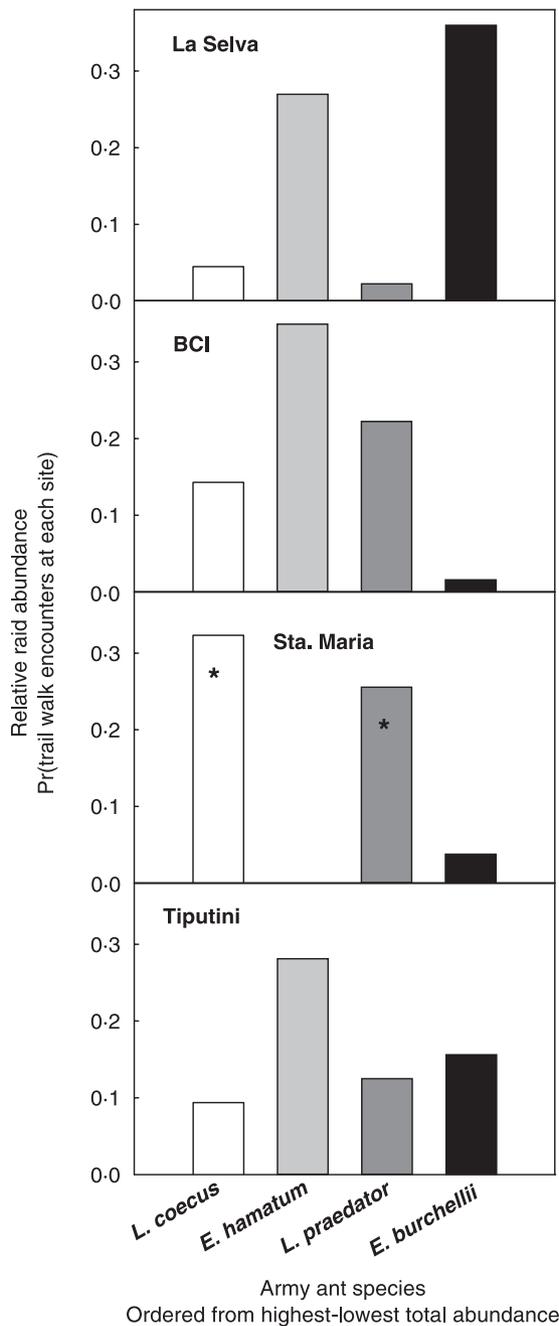


Fig. 4. The relative abundance (proportion of total army ant raid encounters during trail walks) of four common army ant species at four Neotropical forest sampling localities. Species are listed in decreasing order of total abundance summed across sites, and shading of bars represents species identity. Bars with asterisks represent abundances that were significantly different at the indicated site from all of the other sites, according to ANOVA *post-hoc* tests (Tukey HSD). No other differences were significant.

that forage underground (Mirenda *et al.* 1980; Rettenmeyer *et al.* 1983; LaPolla *et al.* 2002; Powell and Clark 2004; O'Donnell, Kaspari and Lattke 2005; Powell and Franks 2006).

Viewed as an organism, army ant colonies are like many terrestrial top predators: they are large bodied, long lived, occur at low densities, and have low rates of

reproduction (Rettenmeyer 1963; Schneirla 1971; Franks 1983). *Eciton burchellii* is affected by forest fragmentation, and populations disappear from small fragments (Franks and Fletcher 1983; Partridge, Britton and Franks 1996; Boswell *et al.* 1998; Meisel 2004). No other guild of predators shares army ants' mass cooperative foraging strategies, although cooperative raiding has evolved convergently in a few genera of ants (Gotwald and Brown 1966; Hölldobler and Wilson 1990). It is unlikely that other predators on arthropods would compensate for the local extinction of army ants in a tropical forest (Menge *et al.* 1994).

SITE DIFFERENCES IN DOMINANT SPECIES ACTIVITY

The four most abundant species differed in their rates of occurrence among sites. These species differ in raid behaviour and diet preferences (Schneirla 1971; Rettenmeyer *et al.* 1983; Powell and Franks 2006). For example, on BCI *E. hamatum* takes predominantly the brood of ants, with a specialization on *Acromyrmex* leaf-cutting ants, while *E. burchellii* preys heavily on *Camponotus* carpenter ants but also takes a diversity of non-ant litter arthropods (Franks 1983; Silva and Höfer 1994; Powell and Franks 2006). Raids of the dominant species generally occurred under similar time and weather conditions among sites. The striking exception was *L. coecus*, which showed relatively high pre-dawn activity at Sta. Maria. These patterns suggest that the relative abundances of a small number of common army ant species may determine the ecological impacts of the army ant community at a given site. The differences in the abundance of the dominant species may explain many of the differences in broad patterns of raid activity that we detected (i.e. for instance, temperature effect on BCI, and the high raid activity at Sta. Maria).

Two sites stand out in terms of the representation of major army ant foraging modes. First, two species of *Labidus* that frequently raid underground were significantly more abundant at Sta. Maria. This suggests an especially heavy pressure on subterranean prey taxa at this site. Second, data from both the trail walks and the plot watches suggest that BCI was relatively low in the abundance of *E. burchellii* and *L. praedator*. Above-ground raids of both of these species attract large mixed flocks of facultatively and obligately associated birds that feed on escaping or partially subdued prey of the army ants (Willis and Oniki 1978; Wrege *et al.* 2005). The low densities of surface raiding species may help explain the documented extinction and decline of some antbirds on BCI (Willis 1974; Robinson 2001), and it may have long-term implications for the remaining antbird community on the island.

Our data suggest that army ant species vary widely in raid activity within sites, with a few species accounting for much of the above-ground raid activity. The dominant species varied significantly in density among

sites. These within and between site raid activity differences, coupled with diet specificity, suggest that army ant communities are not functionally homogeneous, assuming that raid rates correspond to predation pressure. We know of no data on whether and how army ant species affect each other's prey choice and prey capture rates. Interestingly, army ant raid columns of different species frequently meet in tropical forests, and interspecific aggression is limited (Rettenmeyer 1963; Schneirla 1971).

WEATHER AND RAID ACTIVITY

Climatic factors likely influence geographical variation in army ant community structure (Kaspari and O'Donnell 2003). Across the four tropical forests that we sampled, the relationship between raid frequency, local weather, and time of day varied. In particular, the relationships of raid activity with ambient temperature varied significantly among sites. Trail walk raid rates generally covaried with ambient temperature at three sites, but not at Sta. Maria, where raid rates varied inversely with ambient temperature. Furthermore, raid activity was highest in the pre-dawn hours at Sta. Maria, but was highest in the daylight hours, especially in the afternoon, at the other sites.

O'Donnell and Kumar (2006) found decreases in army ant raid rates with elevation in Central America. Sta. Maria had higher army ant densities and species richness, and is higher in elevation than the other sites we sampled. Sta. Maria is lower than the forests sampled by O'Donnell and Kumar (2006). Data on additional intermediate elevation forests are needed to assess the generality of mid-domain effects on army ant density and diversity.

The availability of army ant raids to attending birds and other associates depends in part on the time of day at which they raid. The diel and temperature-related activity rhythms of prey species may also affect their probability of interacting with army ant raids at a given site. Whether and how these activity patterns correspond to army ant raid rates is largely unknown.

Conclusions

We documented significant site variation in army ant species richness and species composition. Perhaps more relevant to the ecological impact of army ants, the relative abundance of the most common species also varied among sites. These patterns of site variation in army ant community composition are associated with dramatic differences in foraging raid activity. Our study demonstrates that relatively rapid sampling with standardized protocols can identify key differences among communities of this poorly understood taxon of top predators. The different sampling methods that we employed (trail walks, plot watches and baited traps) yielded similar estimates of relative rates of foraging raid activity among the sites. At most sites,

army ant raid activity depended on local weather and time of day, but the direction of these relationships varied among sites. Top predators such as army ants often function as ecological keystones, having strong interaction effects on a diversity of species at lower trophic levels (Power *et al.* 1996; Pace *et al.* 1999; Hooper *et al.* 2005). Our data suggest that army ant impacts on their symbionts and prey are geographically heterogeneous in the Neotropics.

Acknowledgements

Primary funding was provided by a grant from the National Geographic Society (M.K., lead PI). Additional support was provided by NSF Grant DEB 0212386 to M.K., NSF grant IBN-0347315 to S.O'D., and a CASE Studentship from the Natural Environment Research Council (NER/S/A/2001/05997), U.K., and the CASE partner, the Smithsonian Tropical Research Institute, Panama to S.P. The following assisted with data collection in the field: B. Baker at BCI; G. Crutsinger at La Selva; A. Kumar and E. Koncsek at Tiputini; and A. Grotto, E. Rodriguez, O. Delgado, A. Rodriguez, D. Kronauer, L. Reyes, and Y. Guevara at Sta. Maria. Thanks to David Romo Vallejo and Kelly Swing for help with arranging and coordinating field work in Ecuador. Vouchers have been deposited at the Department of Zoology, University of Oklahoma, and in the Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela. The editors and two anonymous reviewers made helpful comments on the manuscript.

References

- Agosti, D., Majer, J.D., Alonso, L.E. and Schultz, T.R., eds. (2000) *Measuring and Monitoring Biological Diversity: Standard Methods for Ground-living Ants*. Smithsonian Press, Washington DC.
- Berghoff, S.M., Weissflog, A., Linsenmair, K.E., Hashim, R. and Maschwitz, U. (2002) Foraging of a hypogaean army ant: a long neglected majority. *Insectes Sociaux*, **49**, 133–141.
- Bolton, B. (1995) *A New General Catalogue of the Ants of the World*. Harvard University Press.
- Boswell, G.P., Britton, N.F. and Franks, N.R. (1998) Habitat fragmentation, percolation theory and the conservation of a keystone species. *Proceedings of the Royal Society of London Series B*, **26**, 1921–1925.
- Boswell, G.P., Franks, N.R. and Britton, N.F. (2000) Habitat fragmentation and swarm raiding army ants. *Behaviour and Conservation*, **2**, 141–158.
- Brady, S.G. (2003) Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioural and reproductive adaptations. *Proceedings of the National Academy of Sciences*, **100**, 6575–6579.
- Brose, U., Berlow, E.L. and Martinez, N.D. (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*, **8**, 1317–1325.
- Chao, A., Hwang, W.-H., Chen, Y.-C. and Kuo, C.-Y. (2000) Estimating the number of shared species in two communities. *Statistica Sinica*, **10**, 227–246.
- Chao, A., Chazdon, R.L., Colwell, R.K. and Shen, T.-J. (2005) A new statistical approach for assessing similarity of

- species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. and Tilman, D. (1997) Biotic control over the functioning of ecosystems. *Science*, **277**, 500–504.
- Colwell, R.K., Mao, C.X. and Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.
- Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201–219.
- Estes, J.A. (1995) Top-level carnivores and ecosystem effects: questions and approaches. *Linking Species and Ecosystems* (eds C.G. Jones and J.H. Lawton), pp. 151–158. Chapman and Hall, New York.
- Franks, N.R. (1983) Ecology and population regulation in the army ant *Eciton burchelli*. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (eds E.G.J. Leigh, A.S. Rand and D.M. Windsor), pp. 389–396. Smithsonian Institution Press, Washington DC.
- Franks, N.R. and Bossert, W.H. (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. *Tropical Rain Forest: Ecology and Management*. Special Publication of the British Ecological Society, No. 2 (eds S.L. Sutton, T.C. Whitmore and A.C. Chadwick), pp. 151–163. Blackwell Scientific Publications, Oxford.
- Franks, N.R. and Fletcher, C.R. (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behavioral Ecology and Sociobiology*, **12**, 261–270.
- Gotwald, W.H. Jr (1995) *Army Ants: the Biology of Social Predation*. Comstock Associates, Ithaca.
- Gotwald, W.H. Jr and Brown, W.L. (1966) The ant genus *Simopelta* (Hymenoptera: Formicidae). *Psyche*, **73**, 261–277.
- Hölldobler, B. and Wilson, E.O. (1990) *The Ants*. Harvard University Press.
- Hooper, D.U., Chapin, E.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Jeanne, R.L. (1979) A latitudinal gradient in rates of ant predation. *Ecology*, **60**, 1211–1224.
- Kaspari, M. (1996) Litter ant patchiness at the 1-m(2) scale: disturbance dynamics in three Neotropical forests. *Oecologia*, **107**, 265–273.
- Kaspari, M. and O'Donnell, S. (2003) High rates of army ant raids in the Neotropics and implications for ant colony and community structure. *Evolutionary Ecology Research*, **5**, 933–939.
- Kistner, D.H. (1982) The social insects' bestiary. *Social Insects* (ed. H.R. Hermann), pp. 1–244. Academic Press, New York.
- LaPolla, J.S., Mueller, U.G., Seid, M. and Cover, S.P. (2002) Predation by the army ant *Neivamyrmex rugulosus* on the fungus-growing ant *Trachymyrmex arizonensis*. *Insectes Sociaux*, **49**, 251–256.
- Leigh, E.G. Jr (1999) *Tropical Forest Ecology: a View from Barro Colorado Island*. Oxford University Press, New York.
- McDade, L.A., Bawa, K.S., Hespeneheide, H.A. and Hartshorn, G.S. (1994) *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press.
- Meisel, J.E. (2004) The influence of microclimate and habitat area on the ecology of the army ant *Eciton burchellii* in tropical forest fragments. PhD Dissertation, University of Wisconsin-Madison.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A. and Yamada, S.B. (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, **64**, 249–286.
- Mirenda, J.T., Eakins, D.G., Gravelle, K. and Topoff, H. (1980) Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behavioral Ecology and Sociobiology*, **7**, 119–127.
- O'Donnell, S. and Kumar, A. (2006) Microclimatic factors associated with elevational changes in army ant density in tropical montane forest. *Ecological Entomology*, **31**, 491–498.
- O'Donnell, S., Kaspari, M. and Lattke, J. (2005) Extraordinary predation by the Neotropical army ant *Cheliomyrmex andicola*: implications for the evolution of the army ant syndrome. *Biotropica*, **37**, 706–709.
- Otis, G.W., Santana, C.E., Crawford, D.L. and Higgins, M.L. (1986) The effect of foraging army ants on leaf-litter arthropods. *Biotropica*, **18**, 56–61.
- Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Paine, R.T. (1992) Food-web analysis through field measurements of per-capita interaction strength. *Nature*, **355**, 73–75.
- Partridge, L.W., Britton, N.F. and Franks, N.R. (1996) Army ant population dynamics: the effects of habitat quality and reserve size on population size and time to extinction. *Proceedings of the Royal Society of London Series B*, **263**, 735–741.
- Philpott, S.M. and Armbrrecht, I. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, **31**, 369–377.
- Pinnegar, J.K., Polunin, Francour, N.V.C., Badalamenti, P., Chemello, F., Harmelin-Vivien, R., Hereu, M.-L., Milazzo, B., Zabala, M., D'Anna, M.G. and Pipitone, C. (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*, **27**, 179–200.
- Powell, S. and Clark, E. (2004) Combat between large derived societies: a subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insectes Sociaux*, **51**, 342–351.
- Powell, S. and Franks, N.R. (2006) Ecology and the evolution of worker morphological diversity: a comparative analysis with *Eciton* army ants. *Functional Ecology*, **20**, 1105–1114.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. and Paine, R.T. (1996) Challenges in the quest for keystones: identifying keystone species is difficult – but essential to understanding how loss of species with affect ecosystems. *Bioscience*, **46**, 609–620.
- Quiroz-Robledo, L., Valenzuela-González, J. and Suárez-Landa, T. (2002) Las hormigas Ecitoninas (Formicidae: Ecitoninae) de la Estación de Biología Tropical Los Tuxtlas, Veracruz, México. *Folia Entomologica Mexicana*, **41**, 261–281.
- Raffaelli, D.G. and Hall, S.J. (1996) Assessing the relative importance of trophic links in food webs. *Food Webs: Integration of Patterns and Dynamics* (eds G.A. Polis & K.O. Winemiller), pp. 185–191. Chapman and Hall, New York.
- Rettenmeyer, C.W. (1963) Behavioral studies of army ants. *University of Kansas Scientific Bulletin*, **44**, 281–465.
- Rettenmeyer, C.W., Chadab-Crepet, R., Naumann, M.G. and Morales, L. (1983) Comparative foraging by Neotropical army ants. *Social Insects in the Tropics* (ed. P. Jaisson), pp. 59–73. Université Paris-Nord.
- Robinson, W.D. (2001) Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review. *Animal Biodiversity and Conservation*, **24**, 51–65.
- Schmitz, O.J. (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, **87**, 1432–1437.

- Schneirla, T.C. (1971) *Army Ants: a Study in Social Organization*. W.H. Freeman, New York.
- Shiomoto, A., Tadokoro, K., Nagasawa, K. and Ishida, Y. (1997) Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Marine Ecology Progress Series*, **150**, 75–85.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. and Strohmeier, K. (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, **16**, 269–312.
- Silva, R. and Höfer, H. (1994) Prey spectrum of two army ant species on Central Amazonia, with special attention on the effect on spider populations. *Andrias*, **13**, 189–198.
- Terborgh, J., Lopez, L., Nunez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. and Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.
- Watkins, J.F.I.I. (1976) *The Identification and Distribution of New World Army Ants (Dorylinae: Formicidae)*. Baylor University Press, Waco, TX.
- Weissflog, A., Sternheim, E., Dorow, W.H.O., Berghoff, S. and Maschwitz, U. (2000) How to study subterranean army ants: a novel method for locating and monitoring field populations of the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith (1857) (Formicidae, Dorylinae) with observations on their ecology. *Insectes Sociaux*, **47**, 317–324.
- Willis, E.O. (1974) Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs*, **44**, 153–169.
- Willis, E.O. and Oniki, Y. (1978) Birds and army ants. *Annual Review of Ecology and Systematics*, **9**, 243–263.
- Wootton, J.T. (1997) Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs*, **67**, 45–64.
- Wrege, P.H., Wikelski, M., Mandel, J.T., Rassweiler, T. and Couzin, I.D. (2005) Antbirds parasitize foraging army ants. *Ecology*, **86**, 555–559.

Received 4 December 2006; accepted 26 January 2007

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Numbers of army ant foraging raids encountered at four Neotropical sites.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01221.x>

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.