

Microclimatic factors associated with elevational changes in army ant density in tropical montane forest

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Abstract. 1. The density (rate of encountering foraging raids) and species richness of army ants (Formicidae: Ecitoninae, and behaviourally convergent Ponerinae) was measured in montane tropical forest. Above-ground and subterranean army ant raids were sampled using standard protocols at four sites across an elevational gradient (1200–1650 m above mean sea level) in and near cloud forest in the area of Monteverde, Costa Rica.

2. Mean ambient temperature differed among sites, and decreased with elevation. For the above-ground foraging army ant species, raid rates also declined with elevation. Surface army ant raid rates, however, were not affected by day to day weather variation within sites (temperature, cloud cover, or precipitation).

3. For the underground foraging army ant species, raid rates did not vary directionally with elevation, and subterranean raid rates were not affected by day to day weather variation within sites.

4. Army ant species richness was not directionally related to elevation, and species sharing among sites was generally high.

5. Army ant community structure changes with elevation in Neotropical montane forest, and the results suggest that the strongest effects are of temperature regimes on the density of raids. These findings provide a baseline against which to detect changes in army ant communities that may accompany directional climate change in tropical cloud forests.

Key words. Cloud forest, Costa Rica, Ecitoninae, Monteverde, Ponerinae, species richness.

Introduction

New World army ants belong to the subfamily Ecitoninae, with behaviourally convergent species in the genus *Simopelta* (Gotwald & Brown, 1966; Longino, 2000; Brady, 2003). The dramatic foraging behaviour of the above-ground swarm raiding army ant species *Eciton burchellii* and *Labidus predator* have long attracted the interest of tropical biologists (Darwin, 1839; Wheeler, 1921). There is also a substantial, but relatively poorly studied, subterranean army ant fauna (Weissflog *et al.*, 2000; O'Donnell *et al.*, 2005). Among ants, army ants exhibit a unique type of mass foraging behaviour that involves the co-

ordination of raid parties of thousands to hundreds of thousands of workers. The workers in a raid party cooperate to locate, subdue, and harvest prey. Mass foraging makes the army ants highly successful top predators in tropical forests (Gotwald, 1995). As such, army ants function as ecological keystones (Franks & Bossert, 1983; Boswell *et al.*, 1998, 2000).

Army ants are of special interest from a conservation standpoint for two reasons. First, army ant colonies are nomadic (Gotwald, 1995; Brady, 2003). They do not construct or occupy permanent homeostatic nests, and thus they are more directly exposed to local climatic variation than other social insect taxa. For this reason, army ants may serve as particularly sensitive indicators of climatic variation and, possibly, of directional climate change. Second, because army ants are top predators, they affect the evolution and community composition of their prey (Franks, 1982a; Rettenmeyer *et al.*, 1983; Otis *et al.*, 1986).

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Furthermore, army ants support an array of symbiotically associated vertebrate and invertebrate species (Schneirla, 1971; Willis & Oniki, 1978; Kistner, 1982). Because army ants influence a diversity of other species, factors that affect army ant community composition will likely result in cascading effects on their ecosystems (Ebenman & Jonsson, 2005).

When foraging, army ant colonies are conspicuous and can be sampled using straightforward methods (Berghoff *et al.*, 2002; Kaspari & O'Donnell, 2003). Recent studies suggest that army ant communities are diverse in species composition, and that army ant raids occur at much higher rates than previously recognised. Neotropical lowland wet forest sites can support army ant communities of approximately 20 species (Rettenmeyer *et al.*, 1983; Quiroz-Robledo *et al.*, 2002). Summed across all army ant species, raids occur on the order of one raid per square meter of forest floor per day in Neotropical forests (Kaspari & O'Donnell, 2003). Army ant raid rates vary positively with primary plant productivity (strongly linked to local climate) among sites, suggesting that climatic factors influence army ant community structure (Kaspari & O'Donnell, 2003). Nearly all rigorous army ant research to date, however, has been conducted at a few, well-studied lowland forest sites (Franks, 1982a; Otis *et al.*, 1986; Bierregaard & Lovejoy, 2003; Powell & Clark, 2004). Consequently, information on how army ant communities vary with elevation is lacking, and relatively little is known about the density and diversity of army ants in higher elevation tropical forests (Roberts *et al.*, 2000; Schöning *et al.*, 2005).

The aim of this study was to test the prediction that elevational changes in microclimate affect army ant community composition. Primary productivity generally declines with elevation in montane forest ecosystems (Wang *et al.*, 2003). Based on the findings of an earlier study of army ant activity across a wide geographic range (Kaspari & O'Donnell, 2003), it was predicted that army ant raid rates would decline with elevation

in tropical montane forest. Army ant density and diversity, and microclimatic variation, were sampled using standardised methods at four sites at elevations ranging from 1200 m to 1650 m above sea level near Monteverde, Costa Rica. Sample sites were chosen to span different biotic life zones (Table 1; Holdridge, 1966). Turnover of biotic life zones occurs over short linear distances and with relatively small changes in elevation in the Monteverde area (Bolaños & Watson, 1993; Haber, 2000). The community composition of vascular plants, birds, and amphibians and reptiles change dramatically over the sampled elevational range (Haber *et al.*, 1996; Pounds *et al.*, 1997; Young & McDonald, 2000; also see appendices in Nadkarni & Wheelwright, 2000).

The following questions were addressed: (i) How is the rate of foraging activity of a site's army ant fauna related to microclimatic variation across elevation? (ii) How does the species composition of the montane forest army ant community change with elevation? To answer these questions the relationships of microhabitat variables (weather: precipitation, temperature, and cloud cover; forest cover; and topography) with army ant density and species richness were analysed.

Methods

Sampling sites and dates

Data were collected at four sites separated by > 500 m linear distance (Table 1). The sites differed in elevation above sea level. Three of the sites were on the Pacific slope: Bajo del Tigre, Maxson-Morrison properties, and Monteverde Cloud Forest Reserve, henceforth MVCFR (Clark *et al.*, 2000). The remaining site (San Gerardo) was on the Atlantic slope. All data were collected in 2005; dates of sampling largely overlapped

Table 1. Sites sampled with trail walks for army ant activity in Monteverde, Costa Rica. Biotic life zones according to Haber (2000). For each site, weather characteristics during trail walk samples are listed.

Site, coordinates of walks and life zone	Approximate elevation (m above sea level)	Mean air temp °C ± SD during trail walks*	Air temp. range (°C) during trail walks	% of walks overcast	% with mist
San Gerardo 10°21.855'N 84°47.375'W Premontane rain forest	1200	17.5 ± 1.8A,B	14.9–20.2	86	50
Bajo del Tigre 10°18.320'N 84°49.002'W Premontane wet forest	1350	18.8 ± 2.5A	15.1–24.4	14	21
Maxson-Morrison 10°18.156'N 84°48.113'W Lower montane wet forest	1500	16.8 ± 2.2B	14.3–21.7	33	24
MVCFR 10°18.154'N 84°47.727'W Lower montane wet forest/ Lower montane rain forest	1650	16.3 ± 1.9B	13.2–21.2	44	31

*Postscripts indicate temperature means that differed significantly ($P < 0.05$) according to ANOVA followed by Tukey's HSD post-hoc comparison.

among the sites (San Gerardo: 11 January–5 March; Bajo del Tigre: 12 January–1 March; Maxson-Morrison: 21 January–28 February; MVCFR: 17 January–2 March).

Trail habitat surveys

Prior to sampling, one or more trails were chosen to walk for the purpose of sampling army ant occurrence at each site. All trails were located in forest reserves, or on forested private property contiguous with reserves. 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 1.5 km to 2.3 km in length. Trailside vegetation and leaf litter were cleared when necessary to provide a clear, open path at least 0.5 m wide with an unobstructed view of the ground.

Along each trail habitat characteristics were measured every 20 m. For each habitat characteristics sample forest cover (three categories: primary forest, second growth, or open, e.g. treefall gap or clearing) and topography [five categories: level, slope (> 10%), ridge top (slopes of > 10% within 5 m on both sides of trail), cliff edge (slope > 50% with 5 m of trail), or streamside (stream within 5 m of trail)] were recorded. The associations of army ant raid encounters with forest cover, and with topography, were tested using a Goodness of Fit contingency test with William's correction (Sokal & Rohlf, 1981).

Trail walks

Above-ground army ant foraging activity is readily detected by observers because the ants move in co-ordinated columns or swarms across the surface of the forest floor. Above-ground army ant activity was recorded while walking the surveyed trails at speeds of approximately 1 km h⁻¹. A maximum of one walk was conducted per site per calendar day. Walks started in the morning (08.30–10.50 h), afternoon (12.30–16.30 h), and at night (19.00 h). At the start of every walk the following were noted: which trail was being sampled, time to nearest minute, air temperature (all temperatures were taken to the nearest 0.1 °C with a digital thermometer), and current weather conditions (sky: clear or overcast; and precipitation: whether or not mist was falling). A small number of walks at each site (≤ 5 per site) were cancelled during periods of heavy rainfall. During trail walks the ground was scanned continuously for army ant activity, and data and voucher specimens were collected whenever army ants were encountered. Upon encounters, time to the nearest minute, forest type, and topography (as in habitat surveys, above) were recorded. At the end of each walk time and air temperature were noted. Opportunistic army ant encounters at the sampling sites were also noted. Relationships of sample site and weather variables with the rate of army ant raid encounters were tested using general linear models (GLM) implemented in SAS version 9.1.

Underground baited traps

One hundred oil-baited pitfall traps were placed at each elevation (10 transects of 10 traps each, with a maximum of one

transect per site per calendar day) to sample underground army ant activity (Weissflog *et al.*, 2000; Berghoff *et al.*, 2002). The traps were baited with oil expressed from canned tuna fish. The traps consisted of either PVC pipe or plastic cups, 13 cm tall and 8 cm in diameter. Eight 1 cm diameter holes were drilled or burned through the walls of each trap: four equidistant holes 4 cm up from the bottom and four equidistant holes 4 cm down from the top of the trap. To place the traps, a hole was dug 15 cm deep with a bulb planter, the bottom and sides of the hole were baited with 2 ml tuna oil, and the trap was inserted. The bottom of each trap was filled with dish soap solution in water to capture ants that entered the traps, and then the trap's inner walls were baited with another 2 ml tuna oil. An inverted plastic plate was placed loosely atop each trap to exclude rain, but to permit ants walking on the soil to enter. At each elevation five transects were sampled during daylight hours (diurnal traps were in place for approximately 11 h; traps were set between 06.00 h and 7.30 h, and harvested between 16.30 h and 18.30 h) and five transects overnight (nocturnal traps were in place for approximately 13 h; traps were set between 17.10 and 18.00 h, and harvested between 06.00 h and 07.30 h). When setting the traps start and end time, weather conditions and air temperature were noted. When harvesting, the traps were removed and whether ants were present either in the soapy water or in the trap hole was noted. Ants were collected as vouchers into 70% ethanol. When harvesting the traps start and end time, weather conditions and air temperature were noted.

Quantifying species richness

Species richness data were analysed using EstimateS software (R.K. Colwell: ESTIMATES 7.5, <http://viceroy.eeb.uconn.edu/EstimateS>). Mao Tau, the number of army ant species expected for a given number of raid encounters, was calculated from the observations at each site and plotted to generate species accumulation curves (Colwell *et al.*, 2004). Extrapolations of species richness at each site were made using the Abundance-based Coverage Estimator (ACE; Chao *et al.*, 2000). Chao's abundance-based Jaccard index of species overlap was used to estimate 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 species shared among the two sites (Chao *et al.*, 2005). Voucher specimens have been deposited in the collection of John T. Longino (Evergreen State College) and in the personal collection of S.O'D.

Results

Army ant fauna

Density and diversity of all species of the ant subfamily Ecitoninae, as well as ecologically and behaviourally convergent ants in the genus *Simopelta* (subfamily Ponerinae), were recorded. Ten species of army ants were observed belonging to

four genera (Table 2). One species (*Neivamyrmex antillana*) was collected only in the bait traps, one species (*Labidus coecus*) was collected both in traps and on trail walks, and the remainder were collected only on trail walks. All army ant encounters were of raid fronts, or of columns of ants carrying

Table 2. Records of encounters of army ants in Monteverde, Costa Rica, listed by species. The total number of encounters is given beneath each species name. Species in bold text were encountered at all elevations. For each species, sites with records are in **bold** text.

Species	Site	Trail walk encounters (opportunistic)	Bait trap encounters
<i>Eciton burchellii</i> Total <i>n</i> = 36	San Ger.	5 (10)	0
	Bajo Tigre	8 (5)	0
	Max-Morr.	1 (2)	0
	MVCFR	0 (5)	0
<i>Eciton mexicanum</i> Total <i>n</i> = 12	San Ger.	1 (1)	0
	Bajo Tigre	0 (2)	0
	Max-Morr.	6 (0)	0
	MVCFR	1 (1)	0
<i>Labidus coecus</i> Total <i>n</i> = 20	San Ger.	1 (0)	1
	Bajo Tigre	0 (0)	8
	Max-Morr.	0 (2)	5
	MVCFR	0 (0)	3
<i>Labidus praedator</i> * Total <i>n</i> = 6	San Ger.	0 (0)	0
	Bajo Tigre	2 (1)	0
	Max-Morr.	0 (3)	0
	MVCFR	0 (0)	0
<i>Labidus spininodis</i> Total <i>n</i> = 2	San Ger.	1 (0)	0
	Bajo Tigre	0 (0)	0
	Max-Morr.	1 (0)	0
	MVCFR	0 (1)	0
<i>Neivamyrmex antillana</i> Total <i>n</i> = 2	San Ger.	0 (0)	0
	Bajo Tigre	0 (0)	1
	Max-Morr.	0 (0)	1
	MVCFR	0 (0)	0
<i>Neivamyrmex sumichrasti</i> Total <i>n</i> = 7	San Ger.	0 (4)	0
	Bajo Tigre	1 (0)	0
	Max-Morr.	0 (1)	0
	MVCFR	1 (0)	0
<i>Simopelta JTL-001</i> † Total <i>n</i> = 3	San Ger.	3 (0)	0
	Bajo Tigre	0 (0)	0
	Max-Morr.	0 (0)	0
	MVCFR	0 (0)	0
<i>Simopelta JTL-002</i> † Total <i>n</i> = 2	San Ger.	0 (0)	0
	Bajo Tigre	0 (0)	0
	Max-Morr.	1 (0)	0
	MVCFR	0 (1)	0
<i>Simopelta JTL-004</i> † Total <i>n</i> = 2	San Ger.	2 (0)	0
	Bajo Tigre	0 (0)	0
	Max-Morr.	0 (0)	0
	MVCFR	0 (0)	0

**Labidus praedator* workers from the Monteverde area exhibit characteristics indicating that they may be a species distinct from lower elevation populations. Collected samples have been identified as *L. praedator* population JTL-001 (J. Longino, pers. comm.). †*Simopelta* species nomenclature is uncertain. The specimens have been tentatively assigned to three morphospecies (J. Longino, pers. comm.).

prey. No emigration columns of army ants carrying their own brood were encountered.

Trail walks

During 63 trail walks, totalling a distance of 109.4 km and 108.9 h of search time, army ants were encountered 35 times (overall encounter rates 0.32 raids km⁻¹, 0.32 raids h⁻¹).

The sites differed significantly in the per-km rate of army ant encounters ($F_{3,52} = 2.90$, $P = 0.04$; Table 3). Total army ant encounter rates during trail walks declined with elevation (Fig. 1). Air temperatures recorded during walks varied significantly among the sites (GLM, $F_{3,58} = 4.03$, $P = 0.01$), and air temperatures generally declined with elevation (Table 1). Air temperature variation did not affect encounter rates within sites ($F_{1,52} = 1.72$, $P = 0.20$).

Time of day did not significantly affect the rate of encountering raids ($F_{2,50} = 1.06$, $P = 0.35$), and weather variables had little effect on the probability of encountering army ants during trail walks. The per-km rate of encountering army ants was not significantly related to precipitation ($F_{1,52} = 2.74$, $P = 0.10$), nor to sky conditions ($F_{1,52} = 0.41$, $P = 0.53$).

Above-ground army ants showed little evidence of habitat selectivity when foraging. Raid activity observed during trail walks was not significantly biased at any site among forest cover types (San Gerardo: $G = 0.7$, d.f. = 2, $P > 0.5$; Bajo Tigre: $G = 3.4$, d.f. = 2, $P > 0.1$; Maxson-Morrison: $G = 2.3$, d.f. = 2, $P > 0.25$; MVCFR: $G = 5.2$, d.f. = 2, $0.1 > P > 0.05$), nor among topographies (San Gerardo: $G = 8.4$, d.f. = 4, $0.1 > P > 0.05$; Bajo Tigre: $G = 1.9$, d.f. = 3, $P > 0.5$; Maxson-Morrison: $G = 1.3$, d.f. = 3, $P > 0.5$; MVCFR: $G = 1.2$, d.f. = 4, $P > 0.75$).

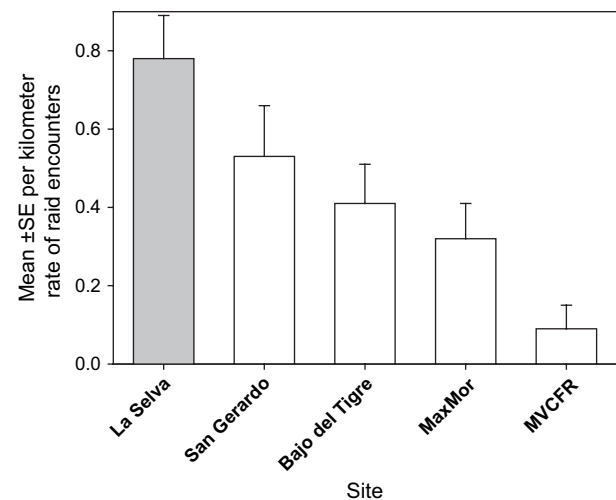


Fig. 1. Mean ± SE per-km rates of encountering army ants during trail walks at four sites near Monteverde, Costa Rica. Data from La Selva (shaded bar) were collected as part of a different study but using the same protocol, and are included for purposes of comparison.

Table 3. Sampling effort and rates of army ant encounters during trail walk surveys in Monteverde, Costa Rica.

Site	Number of walks	Total distance (km)	Total time (h)	Number of army ant encounters	Army ant encounters per walk*	Army ant encounters per km	Army ant encounters per hour
San Gerardo	14	28.4	29.2	13	0.93A	0.46	0.45
Bajo del Tigre	14	26.2	23.8	11	0.79A	0.42	0.46
Maxson-Morrison	19	25.5	32.8	9	0.47A,B	0.36	0.27
MVCFR	16	29.3	23.1	2	0.13B	0.07	0.09

*Postscripts indicate encounter rates that differed significantly ($P < 0.05$) according to ANOVA followed by Tukey's HSD post-hoc comparison.

Baited traps

Subterranean foraging army ants were encountered in baited traps at each site (Table 4).

The overall analysis of site and climatic effects (sky conditions, precipitation, and temperature) on rates of bait trap captures was not significant ($F_{8,26} = 1.91, P = 0.10$). There was, however, a trend toward site differences in bait trap capture rates (GLM, $F_{3,26} = 2.82, P = 0.059$). On the Pacific slope, bait trap capture rates declined with elevation, but the lowest capture rates were at San Gerardo, the lowest elevation site on the Atlantic slope.

Patterns of species richness

Army ant species richness did not show directional changes with elevation. Combining trail walk and bait trap samples, the largest numbers of species ($n = 6$) were recorded at the San Gerardo and Maxson-Morrison sites (Table 2), and the smallest number ($n = 3$) at the MVCFR site. Four of the army ant species were observed at all sites. The *Simopelta* species showed the strongest segregation by elevation. Two *Simopelta* species were recorded only at San Gerardo, while the other was recorded only at the two highest elevation sites (Table 1). Although the species accumulation curve for Bajo del Tigre is lower than for the other sites (Fig. 2a), its 95% confidence intervals overlap the mean values for all of the other sites, suggesting that species richness differences are not significant. Extrapolations of species richness (ACE) suggest similar numbers of species at three of the sites [Fig. 2b; estimated number of species (EstN) is value

of ACE at final sample: San Gerardo EstN = 7.4 species; Bajo del Tigre EstN = 7.0 species; MVCFR EstN = 6.7 species]. The extrapolated species richness was much higher for the Maxson-Morrison site (EstN = 13.4 species).

Table 4. Rates of capture of ants in underground baited pitfall traps in Monteverde, Costa Rica.

Site	% of all traps with ants	% of all traps with army ants (time period of capture)	% of ant captures that were army ants
San Gerardo	65	1 (1 day)	1.6
Bajo del Tigre	42	9 (4 day, 5 night)	21.4
Maxson-Morrison	37	6 (2 day, 4 night)	16.2
MVCFR	49	3 (1 day, 2 night)	6.1

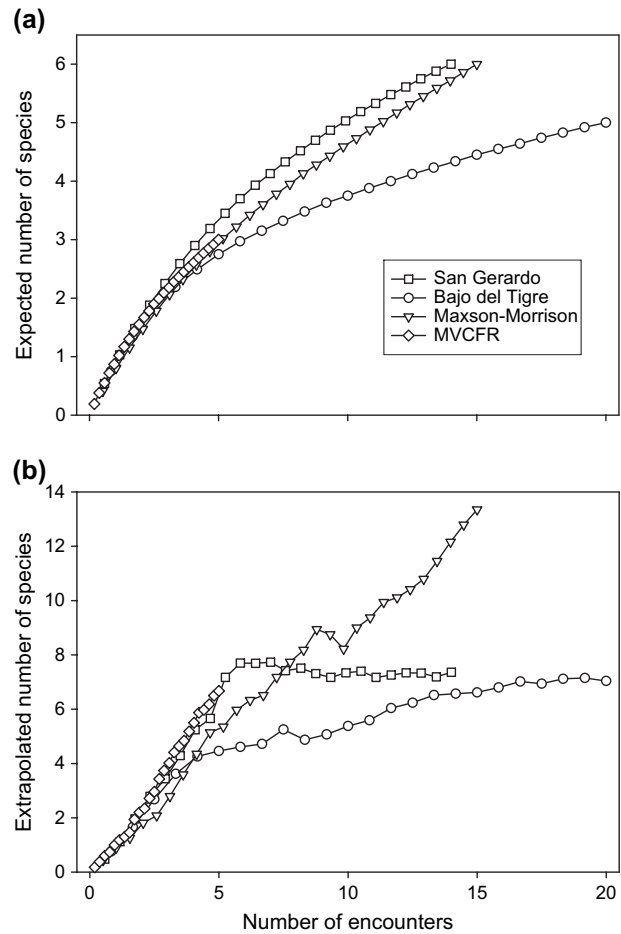


Fig. 2. (a) Expected number of species of army ants plotted against sampling effort (number of raids observed) for four sites in the area of Monteverde, Costa Rica. (b) Extrapolated expected number of species of army ants (Abundance-based Coverage Estimator) plotted against sampling effort (number of raids observed) for four sites in the area of Monteverde, Costa Rica.

Table 5. Observed and estimated overlap of army ant species among four sites in Monteverde, Costa Rica.

Site 1	Site 2	Observed no. of shared species	Chao estimated no. shared	Chao–Jaccard Index
SanGer	Bajo Tigre	2	2.0	0.44
Bajo Tigre	MaxMor	3	6.0	0.43
MaxMor	MVCFR	2	2.8	0.62
SanGer	MaxMor	4	15.3	0.59
Bajo Tigre	MVCFR	2	2.7	0.40
MVCFR	SanGer	2	2.3	0.20

Overlap of species composition was generally high among sites (Table 5). The estimated probability that randomly chosen army ant encounters from each of two sites would be from shared species was lowest for San Gerardo and MVCFR ($Pr = 0.20$), the two sites most widely separated in elevation, but was 0.4 or above for all other pairs of sites (Table 5). Observed numbers of shared species ranged from two to four; the estimated numbers of shared species ranged from 2.0 to 15.3 (Table 5). For four of the six pairs of sites, the observed number of shared species including opportunistic encounters exceeded the estimated number of shared species. Neither observed nor estimated rates of species sharing among sites was consistently related to elevation differences (Table 5).

Discussion

Elevation, weather, microhabitat, and raid activity

Ant communities show dramatic decreases in species richness and density with elevation in montane forests across a range of latitudes (Bruehl *et al.*, 1999; Fisher, 2002; Gotelli & Ellison, 2002). In this study, above-ground army ant foraging raid activity decreased with elevation in the Monteverde area. Furthermore, the highest recorded encounter rates were lower than army ant encounter rates (0.78 raids km^{-1}) recorded in Costa Rica at the La Selva Biological Station at 50 m elevation using the same protocol (S. O'Donnell, M. Kaspari, & J. Lattke, unpublished data). This pattern of elevational declines in army ant raid rates accords with earlier findings from forest floor plot observations, which showed that army ant raid activity covaried positively with net primary productivity (NPP) and with the density of ant colonies nesting in the leaf litter (Kaspari & O'Donnell, 2003). Both NPP and litter ant density are expected to decrease with elevation in tropical montane forest (Kaspari *et al.*, 2000; Longino, 2000). Lower encounter rates at higher elevations could have been caused either by lower army ant colony densities, or by lower army ant foraging activity levels. Army ant foraging activity may be restricted by low temperatures and low insolation at higher elevations. No evidence was found, however, to support weather effects on army ant activity within sites.

Army ants may exhibit local genetic and/or physiological adaptation to ambient temperature regimes. Male army ants are large bodied and may fly long distances on mating flights

(Gotwald, 1995), and army ant queens mate multiply (Denny *et al.*, 2004). The fact, however, that army ant colonies reproduce by colony fissioning, with wingless daughter queens walking to emigrate from their natal colony, means that army ant fecundity is low. There is potential for local genetic differentiation among matriline. Therefore, local adaptation to abiotic thermal conditions (e.g. Harrison *et al.*, 1996) is plausible for army ants.

There was no evidence that army ants were selective among forest cover categories, nor among topographies, when foraging. Raiding army ants did not avoid treefall gaps or other open areas, and raids regularly traversed slopes. The quantitative data were collected in protected, contiguous forest areas, but raid columns were observed crossing roads during opportunistic encounters. It is not known whether or how habitat alteration, particularly forest clearing, affects army ant behaviour and density in the Monteverde area. In lowland tropical forests, *E. burchellii* populations decline following habitat fragmentation (Partridge *et al.*, 1996; Boswell *et al.*, 1998). Some army ant species disappear from forest fragments and small islands (Franks & Fletcher, 1983; Lovejoy *et al.*, 1984; Partridge *et al.*, 1996). Meisel (2004) noted that prey availability can limit army ant colony residence in forest fragments, and also found that higher temperatures in open areas limited the ability of *E. burchellii* raids to cross clearings in lowland forest. Roberts *et al.* (2000) assessed the distribution of the swarm-raiding army ants *E. burchellii* and *Labidus praedator* in intact pre-montane moist forest, shade coffee plantations, and sun coffee plantations. Neither species was seen foraging in sun coffee plantations, suggesting that habitat alteration can affect surface-raiding army ant behaviour in montane forest. Army ants are highly mobile because they do not occupy a permanent nest, and consequently they require extensive areas over which to move and forage (Franks, 1982b; Franks & Fletcher, 1983; Partridge *et al.*, 1996; Swartz, 1997). If forest removal and fragmentation restricts the area over which colonies can forage, it may negatively impact their survival rate.

Species richness

Few clear patterns of elevational segregation of army ant species were seen. Many species spanned part or all of the sampled elevational range, and there was little evidence that the upper elevation (approximately 1650 m) limited the diversity of the army ant community. Additional species of army ants are known to occur adjacent to the Monteverde sample sites, but at lower elevations, on the Atlantic slope. For example, both *Eciton lucanoides* and *E. hamatum* occur at and below approximately 1000 m elevation, below the San Gerardo site and in the Peñas Blancas valley below the MVCFR (S. O'Donnell & A. Kumar, pers. obs.). Little is known about what factors limit the elevational distribution of army ant species, but temperature regimes may play a part. The ant fauna of the Monteverde area is characterized by a large proportion of dark bodied species (Longino, 2000). Dark coloration may aid heating via the absorption of radiant energy, increasing the potential amount of worker activity under the cool, overcast conditions that typify tropical montane forests. Workers of both of the above noted *Eciton* species

that occur below Monteverde are pale in colour relative to Monteverde area congeners.

Implications of the findings

Army ants are top predators in the tropical forest leaf litter, akin to jaguars and harpy eagles on a small scale (Terborgh, 1988; Wilson, 1990). Army ant raids may locally depress populations of dominant prey species in the litter, and in the process free up resources for other species (Franks, 1982a; Otis *et al.*, 1986). Furthermore, army ants support a rich variety of obligate and facultative associates (e.g. mites, beetles, flies, and birds: Elzinga and Rettenmeyer, 1975; Willis and Oniki, 1978; Kistner, 1982). The local extinction of an army ant species may extirpate its associates, and reshape the competitive balance of other species. Lower army ant encounter rates at higher elevations have implications for species that associate with the ants, including ant-following birds (Willis & Oniki, 1978; Hilty, 2005). Future studies could focus on how elevational changes in army ant density influence the exploitation of army ant raids by birds and other facultative associates.

Tropical montane forests, particularly cloud forests, are globally threatened ecosystems that harbour high biodiversity and large numbers of endemic species (Leo, 1995). Cloud forests are particularly sensitive to directional climate change (Pounds *et al.*, 1999). Understanding elevational effects on top predators such as army ants provides an important method for detecting and predicting climate effects in montane tropical forests. The data from this study provide a baseline against which to detect directional changes in army ant communities that could be associated with directional climate change in the Monteverde area (Pounds *et al.*, 1999).

Acknowledgements

Thanks to Jack Longino for advice in the field and for assistance with species identifications. Two anonymous reviewers made helpful comments on an earlier version of the paper. Susan Bulova and Siobhan O'Donnell assisted with field data collection. The Monteverde Conservation League and the Tropical Science Center (MVCFR), and Bobby Maxson, Laura Pfaeffle, Fred Morrison and Laurie Sanders gave permission to work on their property. We are grateful to Frank Joyce and Katy van Dusen for ongoing logistical support. Data were collected under research permits from MINAE, Costa Rica, obtained with the help of the Organization for Tropical Studies. Funding was provided by NSF grant NSF-IBN 0347315 to S. O'D., and an Organization for Tropical Studies post-course award to A.K.

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Accepted 6 March 2006

First published online 16 August 2006