Journal of Animal Ecology

Journal of Animal Ecology 2009, **78**, 91–97 doi: 10.1111/j.1365-2656.2008.01483.x

Elevation and forest clearing effects on foraging differ between surface – and subterranean – foraging army ants (Formicidae: Ecitoninae)

Anjali Kumar* and Sean O'Donnell

Animal Behavior Group, Department of Psychology, University of Washington, Box 351525, Seattle, WA 98195-1525, USA

Summary

1. Forest fragmentation often results in a matrix of open areas mixed with patches of forest. Both biotic and abiotic factors can affect consumer species' ability to utilize the altered habitat, especially for species that range over large areas searching for prey.

2. Army ants (Formicidae: Ecitoninae) are highly mobile top predators in terrestrial Neotropical ecosystems. Army ant foraging behaviour is influenced by forest clearing at lowland sites, and clearing can reduce army ant population persistence.

3. Because high temperatures are implicated in hindering above-ground army ant foraging, we predicted that forest clearing effects on army ant foraging would be reduced at higher (cooler) elevations in montane forest. We also predicted that subterranean foraging, employed by some army ant species, would buffer them from the negative effects of forest clearing.

4. We quantified the foraging rates of above-ground and underground foraging army ants at eight sites along an elevational gradient from 1090 to 1540 m a.s.l. We asked whether these two foraging strategies cause a difference in the ability of army ants to forage in open matrix areas relative to elevationally matched forested habitats, and whether elevation predicts open area vs. forest foraging rate differences.

5. As predicted, army ants that forage above-ground had lower foraging rates in open areas, but the open area vs. forest difference declined with elevation. In contrast, underground foragers were not affected by habitat type, and underground foraging rates increased with elevation. Ground surface temperatures were higher in open areas than forested areas. Temperatures declined with elevation, and temperature differences between open and forested areas decreased with elevation.

6. We conclude that army ants that forage above-ground may be restricted to forested areas due to a thermal tolerance threshold, but that they are released from this limitation at higher elevations. We further suggest that underground foraging permits some army ants to persist within modified landscapes. Our findings have implications for the effects of habitat modification and climate change on these top predators.

Key-words: cloud forest, *Eciton burchellii*, fragmentation, *Labidus coecus*, temperature

Introduction

Forest clearing by humans in tropical habitats often results in forest patches surrounded by a matrix of fully or partially treeless habitat (Bierregaard *et al*. 1992; Laurance *et al*. 2001). The ability of forest animals to use matrix habitats is relevant to their population dynamics and community ecology (Boswell, Britton & Franks 1998; Crooks & Soulé 1999; Keyghobadi *et al*. 2005; Ewers & Didham 2006). Matrix use can depend on behavioural, physiological, and morphological characteristics (Laurance *et al*. 2001; Vandermeer & Carvajal 2001). Top predators are often especially sensitive to forest clearing because they require relatively large home ranges (Saunders, Hobbs & Margules 1991; Crooks 2002). Changes in foraging rates by top predators can have complex effects on local communities via biotic interactions, including trophic cascades (Saunders *et al*. 1991; Crooks & Soulé 1999).

Desiccation and other thermal stresses can be important barriers to matrix use. Matrix areas typically have more variable ground temperatures than the surrounding forests, often

*Correspondence author. E-mail: kumar.anja@gmail.com.

with greater temperature maxima in the matrix (Laurance *et al.* 2001; Meisel 2004, 2006). Insects are especially vulnerable to dehydration due to their large surface area to volume ratio, and forest-dwelling insects often lack the physiological capacity to resist dehydration in matrix areas (Delinger 1986; Hadley 1994; Gibbs, Chippindale & Rose 1997; Hoffmann *et al.* 2003). Army ants are insect top predators of the soil and leaf litter in tropical and subtropical forests. Although they forage in groups, raiding army ant workers do not cluster to shield each other from the local thermal environment (Schneirla 1934). Army ant thermal physiology is largely determined at the individual level rather than the group level (Heinrich 1996; Jones, Nanork & Oldroyd 2007). Furthermore, army ant colonies do not occupy permanent nests, moving an average of over 100 m almost daily to exploit new foraging grounds (Franks & Fletcher 1983). Therefore, army ants may be especially sensitive to the abiotic effects of forest clearing. Populations of *Eciton burchellii* Forel, a common above-ground foraging army ant species, show reduced viability in small patches of forest (Franks 1982; Partridge, Britton & Franks 1996; Boswell *et al.* 1998; Meisel 2004, 2006). *Eciton burchellii* colonies cannot cross large open areas in lowland tropical sites, and temperature plays a major role in regulating *E. burchellii* movement patterns (Meisel 2004, 2006).

Unlike *E. burchellii*, many army ant species forage primarily underground (Berghoff *et al.* 2002, O'Donnell *et al.* 2007). Quantitative samples of army ant raid activity suggest that both elevation and foraging substrate (i.e. above- vs. below-ground) could affect army ant habitat use. In montane forest, above-ground raid rates declined with elevation, but underground raid rates did not (O'Donnell & Kumar 2006). Based on these findings, we posited that forest-clearing effects on army ant foraging behaviour may vary with elevation, and with the ants' foraging substrate. As elevation increases, there is a decrease in ambient ground temperatures in open areas, due to adiabatic cooling and to increased cloud cover (Pounds, Fogden & Campbell 1999; Clark, Lawton & Butler 2000). If open area ground temperatures converge on forest ground temperatures at higher elevations, montane army ants may be better able to use matrix habitats in higher elevations (Roberts, Cooper & Petit 2000; O'Donnell & Kumar 2006). Furthermore, underground foraging behaviour may shield some army ant species from the adverse thermal effects of forest clearing.

The first goal of this study was to test whether forest clearing effects on army ant foraging behaviour covary with elevation and with foraging substrate. The second goal was to assess whether ground temperature variation could explain patterns of foraging behaviour. We used standardized protocols to measure the raid activity of two army ant foraging strategies: above-ground and underground raiding (O'Donnell & Kumar 2006). We sampled foraging activity of species with both strategies in paired forested and open sites across a range of eight elevations, and we measured ground surface temperatures at each collection site. We expected temperatures of open and forested habitats to converge at higher elevations, and we expected above-ground raid rates to grow more similar between open and forested habitats with increasing elevation. If underground foraging buffers army ants from surface temperature constraints, we expected underground foraging army ants' use of open and forest habitats to be similar across all elevations.

Methods

STUDY SPECIES AND SITES

We conducted this study from 15 July to 16 September 2006 near Monteverde, Costa Rica (10°5′60″N, 83°25′60′W). We sampled eight sites from 1090 to 1540 m a.s.l. on the Pacific Slope of the Tilarán Mountain Range. Five Holdridge life zones occur within the 600-m elevation range of our study (Holdridge 1966; Haber 2000). Plant assemblages and local climate regimes change dramatically over this elevation range in the Monteverde area, and we previously documented significant changes in army ant raid rates in forests over a similar elevational range in Monteverde (O'Donnell & Kumar 2006). Each site that we sampled included a forested area paired with an adjacent open (pasture or former active pasture) area for sampling by both trail walks (for surface-raiding army ants) and underground baited traps (for underground-raiding army ants). The methods we used sampled the entire above- and below-ground army ant communities, and estimated guild-wide army ant activity (O'Donnell & Kumar 2006; O'Donnell *et al.* 2007).

TRAIL WALKS

Our trail walk protocol was similar to that used in earlier studies of army ant raid activity (O'Donnell & Kumar 2006; O'Donnell *et al.* 2007). For each site, we chose two trails of comparable length, ranging from 1·1 to 1·5 km, one in the open area and one in the forested area. Both trails were no closer than 20 m from the forest edge. For each site, a trail walk in the forested area and a walk in the open area were conducted on the same day, alternating whether forest or open was carried out first. We balanced trail walks between morning (07.00 to 12.00 h) or afternoon (12.01 to 17.00 h) starts. For each site, seven trail walks were conducted in both the forested and open areas for a total of 14 walks per site. A maximum of three sites were sampled per day and the order of trail walks was randomized weekly among the sites. For each walk we recorded the following: (i) ground temperature to the nearest 0·1 °C with a digital thermometer at the start and again at the end of the walk; (ii) elevation in metres above sea level. recorded with a Garmin (Olathe, Kansas, USA) Gecko handheld GPS unit to the nearest metre. Elevation was verified from topographical maps; (iii) habitat type (either forested or open area); and (iv) time elapsed and distance walked. We walked at speed of approximately 1 km h^{-1}, continuously searching the ground for army and raid activity. The length of each trail walked was estimated using a Garmin Gecko handheld GPS unit. We noted when a foraging army ant column or swarm was encountered, and we collected specimens as voucher samples. We also recorded walks where no army ants were encountered. We calculated raids encountered/kilometre for each walk as an estimate of above-ground army ant foraging activity (O'Donnell & Kumar 2006).

BAIT TRANSECTS

The bait trap transect protocol was modified from that employed in a previous study (O'Donnell & Kumar 2006). Since there was no difference in capture rate of below-ground army ants between traps placed during the day vs. the night from previous work carried out in Monteverde (O'Donnell & Kumar 2006), we ran all bait transects during the day. Baited transects were set between 06.43 h and 11.08 h and were left out for an average of 6·57 h before we collected them. The trap was a reverse pitfall, designed to allow ants foraging underground to enter.

We used a bulb planter to bore a hole 10 cm across and 15 cm deep, then placed a 250 mL plastic cup in the hole. We cut four holes in two rows evenly spaced along the circumference of each cup. Traps were baited with 3 mL of tuna oil both under the base as well as 3 mL oil on the inside rim and a plastic plate was placed over the hole (O'Donnell & Kumar 2006; O'Donnell *et al.* 2007). For each site, transects were set in pairs run simultaneously, two in the forested area and two in the open area. We set the traps on a transect in a nine-trap X-shaped arrangement, with two lines of traps crossing at a right angle, and 5 m between individual traps. For each elevation site, a total of 16 transects were set. One site (Finca San Francisco: 1285 m a.s.l.) had 20 transects. Sixteen transects × nine traps per transect is a total of 144 traps per site, 72 in forest and 72 in open area (90 traps in forest and 90 in open area for Finca San Francisco). We ran transects at each site approximately once per week. Traps in transects that were disturbed by animals were not counted, and these transects were repeated.

At the time of setting the traps, we recorded: (i) ground temperature to the nearest 0·1 °C with a digital thermometer; (ii) elevation in metre above sea level recorded with a Garmin (Olathe, Kansas, USA) Gecko handheld GPS unit to the nearest metre. Elevation was verified from topographical maps; and (iii) habitat type (forested or open). Upon trap collection, we noted which traps or trap holes had underground army ant foraging activity, and collected voucher specimens of workers (voucher specimens are held at the University of Washington). We calculated per-trap encounter rates for each transect as a measure of underground army ant raid activity.

DATA ANALYSIS

We did a two-step analysis on each foraging guild to determine first, whether elevation and habitat type explained variation in raid rates, and second, to determine whether ground temperature could account for these patterns. We used repeated measures analysis of variance (ANOVA) to account for making multiple observations at each elevation sampled (SAS Institute SAS 9·1 2006). In the first analysis, the statistical model used raid encounter rates (per kilometre or per trap) as the response variable, and habitat (open or forest) nested within elevation as predictor variables. In the second analysis, we asked whether ground temperature was explained by army ant encounters (yes/no), and habitat (open or forest) nested within elevation as predictor variables.

Table 1. Army ant species recorded during above ground and subterranean raid activity samples in forest and open habitats in the Monteverde area

Species	Number of trail walk encounters	Number of bait trap encounters
Eciton burchellii parvispinum	35	0
Eciton mexicanum	1	0
Eciton vagans angustatum	2	0
Labidus coecus	0	31
Labidus praedator	5	0
Neivamyrmex punctaticeps	0	1
Neivamyrmex sumichrasti	13	0

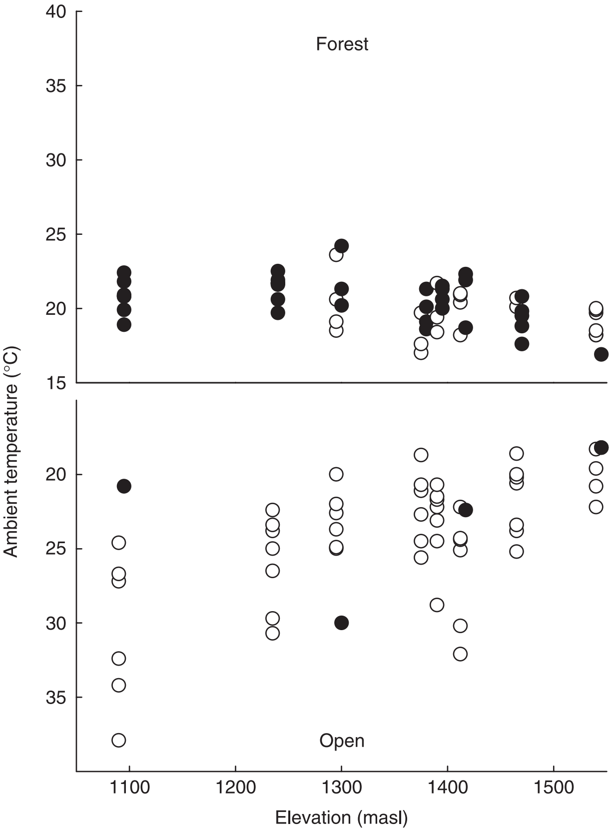

Fig. 1. Ground temperatures recorded during trail walks while sampling for army ant activity in Monteverde, Costa Rica, at different elevations. Filled symbols, walks with army ant encounters; open symbols, walks without army ant encounters. Elevation values of the symbols were adjusted (± 3 m for encounters/no encounters, respectively) so that the data points would not be obscured.

Results

TRAIL WALK SAMPLING OF ABOVE-GROUND FORAGING ACTIVITY

During the 145 km of trail walks, we encountered 56 army ant raid columns; 39 of the 112 trail walks recorded army ant raids. We encountered five army ant species in our trail walk samples (Table 1). Both elevation and habitat type predicted variation in the per-kilometre encounter rate of army ant raid columns (repeated measures ANOVA, overall model: $R^2 = 0·46$, $P < 0·0001$; elevation effect: $F_{14,96} = 2·82$, $P = 0·001$; habitat effect: $F_{1,96} = 42·13$, $P < 0·0001$; Fig. 1). Encounter rate decreased as elevation increased, and army ant raids were seen less often in open areas than forested areas. However, the open/forest difference decreased with elevation, and was reversed at the highest elevation site (Fig. 1).

Forest temperatures ranged from 16·4 to 22·9 °C, while open area temperatures ranged from 19·4 to 36·6 °C. Ground temperatures during trail walks covaried with army ant encounters, habitat, and elevation (overall model: $R^2 = 0·57$,

$P < 0{\cdot}0001$; Fig. 1). Temperatures were lower when army ants were encountered, driven primarily by the fact that more encounters occurred in the forest habitats (mean ± SD for walks with encounters: 20·8 ± 2·2 °C; mean ± SD for walks without encounters: 22·8 ± 4·2; $F_{1,93} = 15{\cdot}8$, $P = 0{\cdot}001$; Fig. 1). After statistically accounting for habitat and elevation effects, temperatures did not differ between walks with and without army ant encounters (type III sums of squares, $F_{1,93} = 0{\cdot}13$, $P = 0{\cdot}72$). Temperatures declined with elevation ($F_{14,93} = 4{\cdot}73$, $P < 0{\cdot}0001$) and temperatures were lower in forest habitats ($F_{1,93} = 43{\cdot}62$, $P < 0{\cdot}0001$). The magnitude of habitat temperature differences decreased with elevation (Fig. 1).

BAIT TRANSECT SAMPLING FOR UNDERGROUND ACTIVITY

Of the 1188 traps we set, 32 collected army ants; 25 of the 132 transects were hit by army ant raids. We encountered two species in our bait trap samples (Table 1). There was no species overlap in the above ground and underground samples.

Elevation, but not habitat type, predicted variation in the per-trap kilometre encounter rate of underground army ant raids (repeated measures ANOVA, overall model: $R^2 = 0{\cdot}35$, $P < 0{\cdot}0001$; Elevation effect: $F_{14,116} = 4{\cdot}53$, $P = 0{\cdot}001$; Habitat effect: $F_{1,116} = 0{\cdot}00$, $P = 1{\cdot}0$; Fig. 2). In contrast with the above-ground activity pattern, soil trap capture rates increased with elevation (Fig. 2).

Ground temperatures during bait trapping covaried with army ant encounters, habitat, and elevation (overall model: $r^2 = 0{\cdot}59$, $P < 0{\cdot}0001$; Fig. 2). Temperatures were lower when army ants were encountered, driven primarily by the fact that more encounters occurred at higher elevations (mean ± SD for transects with encounters: 19·4 ± 2·2 °C, $n = 25$; mean ± SD for transects without encounters: 21·3 ± 3·5; $F_{1,111} = 12{\cdot}3$, $P = 0{\cdot}0007$; Fig. 2). After statistically accounting for habitat and elevation effects, temperatures did not differ between transects with and without army ant encounters (type III sums of squares, $F_{1,111} = 0{\cdot}11$, $P = 0{\cdot}74$). Temperatures declined with elevation ($F_{14,111} = 5{\cdot}1$, $P < 0{\cdot}0001$) and temperatures were lower in forest habitats ($F_{1,111} = 74{\cdot}1$, $P < 0{\cdot}0001$; Fig. 2).

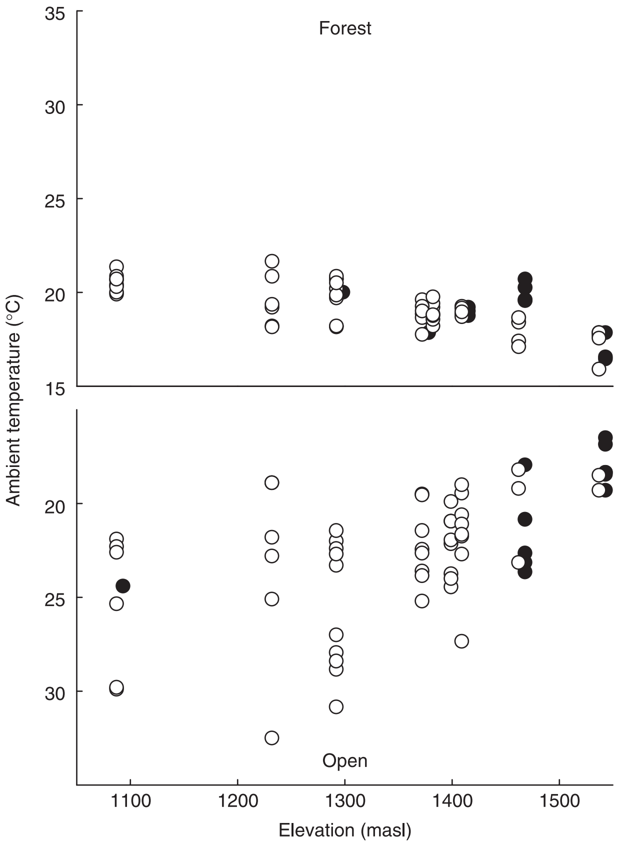

Fig. 2. Ground temperatures recorded at bait transects while sampling for army ant activity in Monteverde, Costa Rica, at different elevations. Filled symbols, transects with army ant encounters; open symbols, transects without army ant encounters. Elevation values of the symbols were adjusted (±3 m for encounters/no encounters, respectively) so that the data points would not be obscured.

Discussion

Patterns of ground temperature covariation with habitat and elevation were associated with rates of above-ground army ant raid activity in our study. Above-ground raids were seen more often in forest than in open areas, but this difference decreased with elevation, as did the temperature difference between the forest and open sites. In contrast, underground raid activity did not correspond to habitat, and instead showed a general increase with elevation. These patterns support our predictions that both underground foraging and increased elevation can buffer the negative thermal effects of forest clearing on army ant activity.

Although data on foraging behaviour are few, army ant species apparently range from strictly surface raiding to strictly underground raiding; some species are intermediate between these extremes (Kronauer *et al.* 2007; O'Donnell *et al.* 2007). However, we saw no species overlap between trail walk and bait trap samples during this study. Our data suggest that foraging substrate can have dramatic effects on habitat use by army ants. We propose that both forest clearing and elevation influence habitat use by surface foragers differently than underground foragers. However, elevation and habitat type are not direct causes of the differential behaviours of army ant foraging patterns. Temperature can affect army ant foraging independently of tree cover (Meisel 2004, 2006). Our data suggest that variation in abiotic factors, such as temperature, directly affect army ant movement and are probably driving the patterns we observed. Additional tests of this hypothesis could include analyses of army ant foraging behaviour in other locations, and with a larger number of species.

ABOVE-GROUND ARMY ANT FORAGING ACTIVITY

Even small clearings within a forest can be barriers to movement for some animal species (Levey *et al.* 2005; Damschen *et al.* 2006). In lowland forests, clearing and fragmentation influence the above-ground foraging behaviour and population longevity of the army ant *E. burchellii* (Partridge *et al.* 1996; Boswell *et al*. 1998; Roberts *et al*. 2000; Meisel 2004, 2006). In our study, above-ground army ant encounter rate covaried with habitat type and elevation. Since army ants are top predators and interact with a large number of invertebrates and vertebrates, the effects of forest clearing on army ant behaviour and population biology are likely to cascade through soil and litter communities. Our data suggest that higher elevations can ameliorate the negative effects of forest clearing that surface-foraging army ants experience. However, above-ground raid rates show a general decline with elevation (O'Donnell & Kumar 2006; this study), and above-ground army ants are rare at elevations higher than those we sampled (J. Longino, personal communication; A. Kumar and S. O'Donnell, personal observations).

Two potentially salient weather patterns change with increasing elevation in tropical montane forests: both temperature and the amount of insolation decline with elevation. Reduced insolation due to frequent cloud cover, and adiabatic cooling, combine to reduce ground temperatures at higher elevations (Pounds *et al*. 1999; Clark *et al*. 2000). Both increased temperatures and direct sunlight have been shown to affect the behaviour of above-ground army ants, with *E. burchellii* avoiding direct sunlight (Roberts *et al*. 2000).

Given the relationship between raid activity and temperature that we observed, and Meisel's (2006) experimental demonstration of temperature effects on *E. burchellii* foragers, ambient temperature is strongly implicated as a factor that explains habitat use by surface army ant raids. Meisel demonstrated that *E. burchellii* located in low elevation tropical forest are likely foraging at their thermal limit. We did not encounter above-ground army ants at temperatures above 30·0 °C. Some species of army ants occur over a wide elevation gradient, suggesting that thermal ecology varies dramatically across their ranges (O'Donnell & Kumar 2006). Surface-raiding army ant populations at higher elevations may be adapted to lower temperatures than lowland populations, and consequently have a lower thermal tolerance than army ants found at lower elevations.

UNDERGROUND ARMY ANT FORAGING ACTIVITY

Underground army ant capture rate was not affected by habitat type, even though ground surface temperatures were higher in the open areas than the forested areas that we sampled. Thermal buffering of subterranean foragers may explain this pattern. Although we did not measure soil temperatures, this factor probably plays an important part in underground foraging behaviour. Soil temperatures can be altered by land-use changes, but diurnal below-ground temperatures are generally lower than above-ground temperatures (Geiger 1965). In tropical montane forests, soil temperatures at depths of 5 to 10 cm are typically cooler than air temperature by 2 to 3 °C during the day, even in open areas (Williams-Linera & Herrera 2003; Campos 2006). Future studies should measure soil temperatures at different periods of the day to produce an accurate profile of the differences in soil and surface temperatures.

We took the temperature readings at our bait transects on the ground surface. The *Labidus coecus* (Latreille) foragers at our baits were usually active at the surface, and this species occasionally comes to the surface when raiding (O'Donnell & Kumar 2006; O'Donnell *et al*. 2007). However, we expect that *L. coecus* foragers are usually buffered from surface temperatures. Our traps' holes reached a maximum depth of 15 cm below soil surface. Although we have no information on the distance from which foragers could detect our bait traps, in most cases, consecutive traps at 5-m distance were not raided simultaneously. Our traps likely sampled army ant foraging activity in and just below the leaf litter (Berghoff *et al*. 2002). However, *L. coecus* is sometimes found raiding at considerable subterranean depths: raids were encountered several metres below the soil surface in wells being dug near the La Selva biological station (J. Longino, personal communication). Soil temperatures at such depths are likely to be highly stable relative to temperatures at the soil surface.

ALTERNATIVES TO TEMPERATURE

In addition to temperature effects, prey availability can influence army ant raid movements (Meisel 2006). While some underground army ant species are thought to be generalist predators, few prey records are available for these species (Rettenmeyer, Naumann & Morales 1983; Perfecto 1992; Berghoff *et al*. 2002). Pasture and open habitats may contain a greater number of ant nests with many individuals, such as *Solenopsis* spp., making open areas more prey rich than forested areas (J. Vandermeer, personal communication). We did not sample prey availability, or prey capture rates, for army ant raids and therefore we cannot rule out habitat differences in prey availability as an alternative hypothesis to explain habitat effects on surface foraging activity. When *E. burchellii* swarms pass through cleared areas in Monteverde, the columns of foragers departing the swarm have been seen carrying prey (Anjali Kumar and Sean O'Donnell, personal observations). Because the raid rate differences between open areas and forest declined with elevation, prey densities would have to show similar patterns of elevational change if they are driving army ant raid rates. Previous studies of density and species richness of insects in matrix habitats and forested areas reveal complex patterns. Some insect groups increase while others decline in matrix relative to adjacent forest (Laurance *et al*. 2001; Schonberg *et al*. 2004).

Another biotic factor that may contribute to the different reactions of above- and below-ground army ant species to habitat type is the interspecific interaction surface raiding army ants have with ant-following birds (Willis & Oniki 1978). Ant following bird species parasitize army ant colonies by stealing large prey items (Wrege *et al*. 2005). It is possible the behavioural adaptations of above- and below-ground foraging and habitat selection could be affected by army ant following birds, even at higher elevations (Kumar & O'Donnell 2007).

Conclusions

We predict that underground army ants will be better able to persist within modified landscapes than surface raiding species. This is important for understanding top predator migration and movement following forest clearing. Directional climate change is manifested by lifting cloud banks, increasing insolation, and elevated temperatures in Neotropical cloud forest (Pounds *et al*. 1999; Nadkarni & Wheelwright 2000; Pounds *et al*. 2006). These abiotic changes may combine with past, and ongoing, forest clearing to negatively impact army ant populations. We expect these changes to affect surface army ant raiding species, as well as their prey and commensal organisms, most strongly.

Acknowledgements

We thank Jim Wolfe, Joe and Jean Stuckey, the Vitosi family, Ecolodge San Luis and the University of Georgia, and the Salazar family for generously allowing use of their private land for this study. Thanks to Yamile Molina and Sebastián Jurado for assistance in the field, and to Frank Joyce and Katy Van Dusen for their continuing logistical support in Monteverde. The Tropical Science Center, Monteverde Conservation League, and The Monteverde Institute extended their help and access to land for this project. Special thanks to Jack Longino for his help with species identification. Research was conducted under permits from the Ministry of the Environment and Energy, Republic of Costa Rica, Scientific Passport # 0387, and in accordance with the laws of the Republic of Costa Rica. Thanks to the Organization for Tropical Studies for ongoing research support, including assistance in obtaining permits. This project was supported by a grant from the University of Washington Royalty Research Fund to S.O'D., and by NSF grant NSF-IBN 0347315 to S.O'D. (Replacement PI Eliot Brenowitz). The research presented was also supported by the National Science Foundation, while S.O'D. was working at the foundation. Any opinions, findings, and the conclusions or recommendations, are those of the authors, and do not necessarily reflect the views of the National Science Foundation.

References

Berghoff, S.M., Weissflog, A., Linsemair, K.E., Hashim, R. & Maschwitz, U. (2002) Foraging of a hypogaeic army ant: a long neglected majority. *Insectes Sociaux*, **49**, 133–141.

Bierregaard, R.O., Lovejoy, T.E., Kapos, V., Agusto dos Santos, A. & Hutchings, R.W. (1992) The biological dynamics of tropical rainforest fragments. *Bioscience*, **42**, 859–866.

Boswell, G.P., Britton, N.F. & Franks, N.R. (1998) Habitat fragmentation, percolation theory, and the conservation of a keystone species. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 1921–1925.

Campos, A. (2006) Response of soil surface CO_2-C flux to land use changes in a tropical cloud forest (Mexico). *Forest Ecology and Management*, **234**, 305–312.

Clark, K.L., Lawton, R.O. & Butler, P.R. (2000) The physical environment. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (eds N.M. Nadkarni & N.T. Wheelwright), pp. 15–34. Oxford University Press, New York.

Crooks, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, **16**, 488–502.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.

Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. & Levey, D.J. (2006) Corridors increase plant species richness at large scales. *Science*, **313**, 1284–1286.

Delinger, D.L. (1986) Dormancy in tropical insects. *Annual Review of Entomology*, **31**, 239–264.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Franks, N.R. (1982) 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. Leigh, A.S. Rand & D.M. Windsor), pp. 389–395. Smithsonian Institution Press, Washington, DC.

Franks, N.R. & Fletcher, C.R. (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behavioural Ecology and Sociobiology*, **12**, 261–270.

Geiger, R. (1965) *The Climate Near the Ground*. Harvard University Press, Cambridge, Massachusetts.

Gibbs, A.G., Chippindale, A.K. & Rose, M.R. (1997) Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *Journal of Experimental Biology*, **200**, 1821–1832.

Haber, W.A. (2000) Plants and vegetation. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (eds N.M. Nadkarni & N.T. Wheelwright), pp. 29–94. Oxford University Press, New York.

Hadley, N.F. (1994) Ventilatory patterns and respiratory transpiration in adult terrestrial insects. *Physiological Zoology*, **67**, 150–189.

Heinrich, B. (1996) *The Thermal Warriors: Strategies of Insect Survival*. Harvard University Press, Cambridge, Massachusetts.

Hoffmann, A.A., Hallas, R.J., Dean, J.A. & Schiffer, M. (2003) Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science*, **301**, 100–102.

Holdridge, L.R. (1966) The life zone system. *Adansonia*, **6**, 199–203.

Jones, J.C., Nanork, P. & Oldroyd, B.P. (2007) The role of genetic diversity in nest cooling in a wild honey bee, *Apis florea*. *Journal of Comparative Physiology, Series A*, **193**, 159–165.

Keyghobadi, N., Roland, J., Matter, S.F. & Strobeck, C. (2005) Among- and within-patch components of genetic diversity respond at different rates to habitat fragmentation: an empirical approach. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 553–560.

Kronauer, D.J.C., Schöning, C., Vilhelmsen, L.B. & Boosma, J.J. (2007) A molecular phylogeny of *Dorylus* army ants provides evidence for multiple evolutionary transitions in foraging niche. *BMC Evolutionary Biology*, **7**, 56.

Kumar, A. & O'Donnell, S. (2007) Fragmentation and elevation effects on bird-army ant interactions in Neotropical montane forest of Costa Rica. *Journal of Tropical Biology*, **23**, 581–590.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O, Laurance, S.G. & Sampaio, E. (2001) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, **16**, 605–618.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146–148.

Meisel, J.E. (2004) *The influence of microclimate and habitat area on the ecology of the army ant* Eciton burchellii *in tropical forest fragments*. Ph.D. thesis, University of Wisconsin-Madison, Madison, Wisconsin.

Meisel, J.E. (2006) Thermal ecology of the Neotropical army ant *Eciton burchellii*. *Ecological Applications*, **16**, 913–922.

Nadkarni, N.M. & Wheelwright, N.T. (2000) Introduction. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (eds N.M. Nadkarni & N.T. Wheelwright), pp. 1–13. Oxford University Press, New York.

O'Donnell, S. & 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., Lattke, J., Powell, S. & Kaspari, M. (2007) Army ants in four forests: geographic variation in raid rates and species composition. *Journal of Animal Ecology*, **76**, 580–589.

Partridge, L.W., Britton, N.F. & 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 B: Biological Sciences*, **263**, 735–741.

Perfecto, I. (1992) Observations of a *Labidus coecus* (Latreille) underground raid in the central highlands of Costa Rica. *Psyche (Cambridge)*, **99**, 214–220.

Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.

Rettenmeyer, C.W., Naumann, M.G. & Morales, L. (1983) Comparative foraging by neotropical army ants. *Social insects in the tropics, Vol. 2. Proc. 1st Int. Symp. I.U.S.S.I. and Soc. Mex. Entomologia, Coyoyoc, Morelos, Mexico, Nov. 1980* (ed. P. Jaisson), pp. 59–73. Université Paris-Nord, Paris, France.

Roberts, D.L., Cooper, R.J. & Petit, L.J. (2000) Use of premontane moist forest and shade coffee agroecosystems by army ants in western Panama. *Conservation Biology*, **14**, 192–199.

SAS software version 9.1 (2006) SAS Institute, Cary, NC, USA.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of habitat fragmentation: a review. *Conservation Biology*, **5**, 18–32.
Schneirla, T.C. (1934) Raiding and other outstanding phenomena in the behaviour of army ants. *Proceedings of the National Academy of Sciences, USA*, **20**, 316–321.
Schonberg, L.A., Longino, J.T., Nadkarni, N.M. & Yanoviak, S.P. (2004) Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. *Biotropica*, **36**, 402–409.
Vandermeer, J. & Carvajal, R. (2001) Metapopulation dynamics and the quality of the matrix. *American Naturalist*, **158**, 211–220.
Williams-Linera, G. & Herrera, F. (2003) Folivory, herbivores, and environment in the understory of a tropical montane cloud forest. *Biotropica*, **35**, 67–73.
Willis, E.O. & Oniki, Y. (1978) Birds and army ants. *Annual Review of Ecology and Systematics*, **9**, 243–263.
Wrege, P.H., Wikelski, M., Mandel, J.T., Rassweiler, T. & Couzin, I.D. (2005) Antbirds parasitize foraging army ants, *Ecology*, **86**, 555–559.

Received 30 January 2008; accepted 1 September 2008
Handling Editor: Simon Leather