Species and site differences in Neotropical army ant emigration behaviour

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Abstract. 1. Along with large wingless queens and group foraging raids, periodic colony movements or emigrations are a defining feature of army ant behaviour. Emigrations are important because they regulate spacing among colonies, and provide access to new foraging sites.

2. Raid and emigration activity of army ant communities was measured at four Neotropical sites using a standardised sampling protocol. Sampling of emigration activity was carried out throughout the diel cycle.

3. Both raid and emigration activity occurred throughout the day and night. Emigration activity was highest under cover of darkness, but sites and species differed in the diel timing of emigrations. These site and species differences have implications for the evolution of emigration behaviour, as well as for the community ecology of army ants.

Key words. Diel cycle, *Eciton*, Ecitoninae, *Labidus*, *Neivamyrmex*, *Nomamyrmex*.

Introduction

Along with large bodied, wingless queens, two striking and possibly unique behavioural features characterise army ants: group foraging raids with mass recruitment, and periodic nomadic movements between temporary nesting sites, which are termed emigrations (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995; Brady, 2003). Colony nomadism is a defining characteristic of the army ant syndrome of traits, which has persisted since the Neotropical subfamily Ecitoninae's origins in the Cretaceous approximately 100 mya (Wilson, 1958; Brady, 2003). During emigrations, the entire adult population of the colony walks in an unbroken column of ants to the new nest or bivouac site. Larval and/or pupal brood are carried by the workers during an emigration. Species differ in the range of lengths of their emigration trails, but these can be up to 450 m long in *Eciton hamatum* (Schneirla, 1971).

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Many army ants engage in cyclic emigrations that are closely related to brood development, but species vary in the frequency and regularity of the timing of their emigrations (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995). Some species, including those that typically raid underground, spend varying lengths of time in their nest locations (Gotwald, 1995; Powell & Baker, 2008). Other species, notably the well-studied *Eciton burchellii* and *E. hamatum*, exhibit a pattern of regular alternation between two behavioural states, the statary and nomadic phases (Rettenmeyer, 1963; Schneirla, 1971; Teles da Silva, 1977).

Army ant foraging raids and emigrations are closely related both mechanistically and functionally. For example, *E. burchellii* diurnal raids segue directly into emigration columns later in the day, on days when the colony moves (Schneirla, 1971). Emigrations generally follow the path taken by the main raiding column earlier on the same day (Schneirla, 1971; Schöning *et al.*, 2005). During both raids and emigrations, the ants move as a mass in coordinated but leaderless groups, with distinct exploratory and recruitment pheromones employed by the workers (Topoff *et al.*, 1980). In the Neotropics, army ant species vary in their diel patterns of raiding activity. Some species forage largely in daylight hours, and some are crepuscular or nocturnal (Rettenmeyer, 1963; Powell & Baker, 2008). Other species, such as *Nomamyrmex esenbeckii* and members of the genus *Labidus*, show no apparent diel patterns of raid activity

(Rettenmeyer, 1963; O'Donnell & Kumar, 2006; Powell & Baker, 2008).

Less is known about the diel timing of emigration. Most data on the diel timing of emigration activity have been collected opportunistically, and at only a handful of sites (Rettenmeyer, 1963; Schneirla, 1971; Mirenda *et al.*, 1980). Schneirla (1971) suggested that falling light levels toward sunset trigger emigrations, implying that they are restricted to night-time. However, there are records of daytime emigrations by large-colony species whose emigrations last more than 12 h (Rettenmeyer, 1963; Gotwald, 1995; Powell & Baker, 2008). Neighbouring conspecific army ant colonies are not synchronous in their movement activity and brood production, and as a result, their emigrations are often distributed in time (Schneirla, 1945). Little else is known about community-wide patterns of emigration activity. The present study builds on previous observations by employing systematic unbiased sampling (O'Donnell & Kumar, 2006; O'Donnell *et al.*, 2007) of emigration activity. The study design allowed quantification of diel patterns of emigration activity across species. Furthermore, we were able to assess geographic variation in army ant emigration activity by applying similar methods at several sites.

The goal of the present study was to sample community-wide rates of army ant emigration behaviour, along with raiding (foraging) behaviour, at multiple sites that differ in army ant density and species composition (O'Donnell *et al.*, 2007). Standardised protocols were used to measure above-ground emigration and raid activity of army ants at four Neotropical wet forest sites. Sampling was carried out during four time blocks (two diurnal, two nocturnal) that spanned the diel cycle. The diel timing of raids and emigrations was quantified across all species within sites, as well as at the species level. To test for geographic variation in rates and timing of emigration activity, we compared rates of emigration and raiding within and between the study sites, and we assessed whether species differences in raid and emigration rates corresponded with each other. We also asked whether the diel timing of emigration differed among the study sites, and correlational analyses were used to identify temporal and abiotic factors that could affect emigration behaviour within sites.

Methods

Trail walk protocol

As in previous studies of community-wide army ant raid activity, we walked pre-selected trails repeatedly for the purpose of sampling army ant emigration activity (O'Donnell & Kumar, 2006; O'Donnell *et al.*, 2007). Walking trails are effective for detecting army ant emigration activity for several reasons (Rettenmeyer, 1963; Kaspari, 1996; Vidal-Riggs & Chaves-Campos, 2008). First, army ant emigration columns are often roughly linear. Emigrations can travel distances of several hundred metres and the unbroken columns of ants are likely to intersect trails (Rettenmeyer, 1963; Schneirla, 1971; Franks, 1983; Kronauer *et al.*, 2007). Second, emigrations that cross cleared trails are more likely to be detected than those travelling through obscuring leaf litter. 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 emigrating army ants exit a hole on one side of a trail, cross the trail on the surface, and then return underground immediately on the other side (Franks, 1982).

We searched for army ant emigration activity while walking the selected trails at speeds of approximately 1 km h^{-1}. We illuminated the path with headlamps when working at night. 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 time block was: AM dark (02.00–04.55 hours), AM daylight (08.00–10.30 hours), PM daylight (12.30–15.40 hours), and PM dark (19.15–20.15 hours). At the start of every walk we noted which trail we were sampling, 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, partly cloudy, or overcast). If rain was not falling during a walk, we also estimated time since last rain to the nearest hour. A small number of trail 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 identified a column as an emigration, only if workers were carrying their own brood (larvae or pupae). Therefore, we were conservative in assigning emigration status to army ant columns; ants at the beginning and end of emigration columns are not always carrying brood (Schneirla, 1971), and some emigrations may have been labelled as raid columns. Time was recorded to the nearest minute, and we stopped for approximately 10 min to collect data and voucher specimens into 70% ethanol whenever an army ant emigration was encountered. Presence of army ant brood was confirmed by examining the voucher collections. At the end of each walk, time and air temperature was noted.

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

Study sites and dates of data collection

Barro Colorado Island Research Station, Panama (henceforth BCI), 9°09′N, 79°50′W. BCI is a 1500-ha island in the central part of the Panama Canal (Leigh, 1999). Trails sampled secondary forest (>100 years recovery) and primary forest. Elevation range was 60–190 m above sea level. Data from BCI were collected between 20 July and 9 September 2003. We conducted 35 walks. All trails were 3.5 km long and total trail walk distance was 119.8 km.

La Selva Biological Station, Costa Rica (henceforth La Selva), 10°26′N, 83°59′W. 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). The trails sampled old growth forest with slopes <20°. Elevation range was 40–130 m above sea level. Data from La Selva were collected between 11 June and 4 August 2003. We conducted 25 walks. All trails were 4.7 km long and total trail walk distance was 117.5 km.

Santa Maria Valley, Henri Pittier National Park, Venezuela (henceforth Sta. Maria), 10°22′N 67°49′W. Trails traversed a forested valley ranging in elevation from 530 to 840 m above sea level. Sampling was carried out from 1 August to 2 September 2003. We conducted 41 walks. Trails were 1 km to 4.3 km long and total trail walk distance was 63.2 km.

Tiputini Biodiversity Station, Ecuador (henceforth Tiputini), 0°38′S, 76°08′W. This site comprises extensive primary lowland forest adjacent to Yasuni National Park. Trails sampled both seasonally flooded (varzea) and non-inundated (terra firme) forest. Elevation ranged from 190 to 230 m above sea level. Data from Tiputini were collected between 25 September and 16 October 2003. We conducted 21 walks. Trails were 2.8–3 km long and total trail walk distance was 54.7 km.

Opportunistic records

At two sites (BCI and Tiputini), we recorded emigration activity opportunistically when we encountered columns of army ants that were carrying their own brood outside of the standardised trail walk periods. Data collected from opportunistic encounters were similar to trail walk data, as outlined above. These data were not used in quantitative analyses of raid and emigration rates, but they were used to indicate the range of times of day at which species raid and emigrate.

Results

Emigration rates during systematic trail walks

A total of 29 emigrations of 12 species were encountered during systematic sampling. Most emigration encounters were after nightfall, but five emigration columns (one at BCI and four at Sta. Maria) were seen during daylight hours (Fig. 1). Emigration encounter rates per kilometre differed strongly among sample time blocks ($F_{3,106} = 25.7$, $P < 0.0001$; overall time block encounter rates – AM light: 0.019, PM light: 0.023, PM dark: 0.41, AM dark: 0.033). *Post hoc* analysis showed that the PM dark block had higher rates than all other time blocks; no other time block rate differences were significant. The four sites differed highly significantly in their overall per-kilometre rates of emigration encounters ($F_{3,106} = 7.9$, $P < 0.001$). *Post hoc* comparisons did not indicate significant pairwise site differences, but there was a 2.5-fold difference between the lowest overall site encounter rate (at BCI) and the highest (at Tiputini) (Fig. 1; overall site encounter rates – BCI: 0.058, La Selva: 0.060, Sta. Maria: 0.111, Tiputini: 0.146). Furthermore, the sites differed in the diel timing of maximum emigration activity (significant site × time block interaction: $F_{9,106} = 8.4$, $P < 0.0001$). Emigration activity was highest in the PM dark block at all sites except Sta. Maria, where AM dark emigration activity was highest (Fig. 1). An additional site difference was that the rate of emigration encounters in the PM dark block at Tiputini was 2.46 times higher than the next most active site (La Selva; Fig. 1).
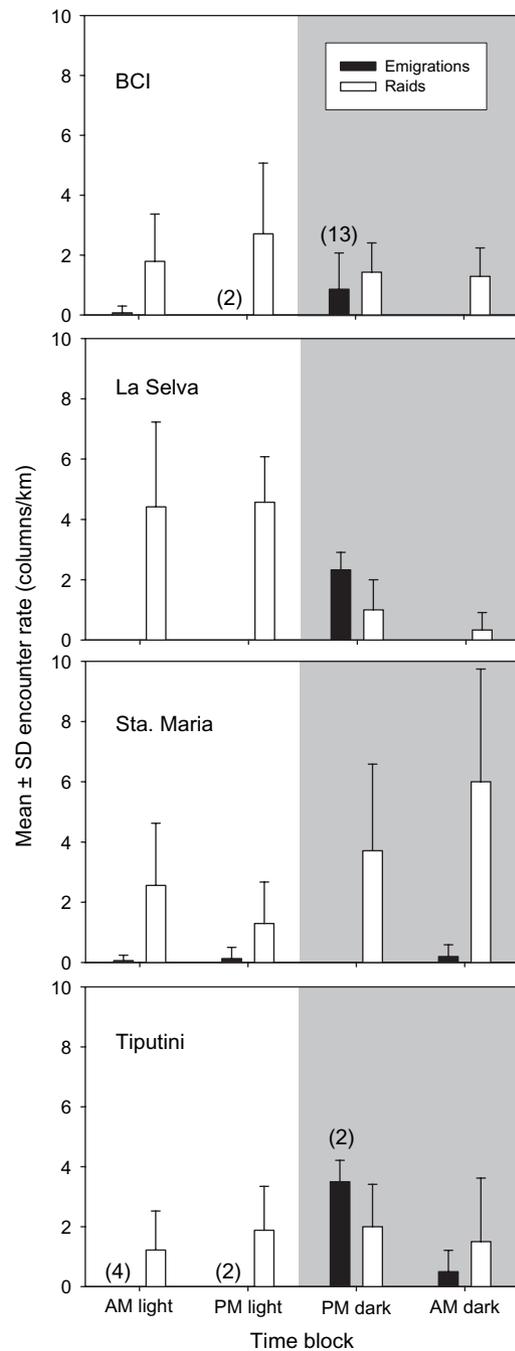

Fig. 1. Vertical bar chart showing mean ± SD rates of encounter of army ant raid (open bars) and emigration (filled bars) columns during standardised trail walks at four Neotropical forest sites. At each site, mean encounter rates are plotted for each of four sampling time blocks at different times of day, with nocturnal time blocks indicated by background grey shading. Numbers of opportunistic emigration encounters for each time block at the BCI and Tiputini sites are indicated in parentheses.

Emigration relationships with foraging behaviour

Raids were encountered at higher rates than emigrations (Fig. 1, after accounting for site effects, $F_{1,236} = 129.5$, $P < 0.0001$). The sites differed significantly in the relative rates of emigration and raid encounters (Fig. 1, $F_{3,236} = 17.4$, $P < 0.0001$). Raid-relative emigration rates (emigrations/raid) were highest at Tiputini (0.26), followed by BCI (0.11), La Selva (0.08) and Sta. Maria (0.05). For species that were encountered during trail walks, the relative abundances of raids and emigrations were positively correlated at three of the study sites (BCI: $n = 9$ species, $r = 0.86$, $P = 0.003$; La Selva: $n = 10$ species, $r = 0.85$, $P = 0.002$; Sta. Maria, $n = 12$ species, $r = 0.59$, $P = 0.04$). However, this relationship did not hold at Tiputini ($n = 11$ species, $r = -0.16$, $P = 0.63$).

We encountered 23 additional emigrations during opportunistic encounters outside the trail walk samples. Eight emigrations at Tiputini belonged to at least four army ant species (Table 1; one sample was lost and was only identified to genus). All four of the identified species were not seen raiding or emigrating during the systematic trail walks at Tiputini (Table 1). Furthermore, most (six of eight) of the opportunistic observations of emigration at Tiputini were made during daylight hours, including two emigrations in the afternoon, falling within the time span of the PM light trail walk period. Opportunistic encounters at BCI yielded an additional 15 emigrations of four species; all but two of these were under cover of darkness.

Diel patterns of emigration activity

Emigration activity for many species was clustered in the early evening hours (Figs 1 and 2). However, we observed 13 emigrations (25% of the total) by at least five species during daylight hours. We observed both raids and emigrations for 13 army ant species during the study (Fig. 2). Pooling across the study sites, emigration activity was heaviest in the night-time hours and raid activity was heaviest during the day, but for many species, both raids and emigrations were widely dispersed across the diel cycle. In our samples, eight species emigrated only at night, two species emigrated day and night, and three emigrated only in the day (Fig. 2).

Abiotic factors

The four sites differed significantly in ambient air temperature during systematic trail walks ($F_{1,103} = 63.0$, $P < 0.0001$), and the time blocks differed significantly in temperature after accounting for site effects ($F_{1,103} = 13.2$, $P < 0.0001$). Sites did not differ in the pattern of temperature change among time blocks (site × time block interaction: $F_{9,103} = 0.73$, $P = 0.68$). After accounting for site and time block effects, temperature did not covary with emigration encounter rate ($F_{1,111} = 0.56$, $P = 0.46$).

The sky was clear during at least seven (54%) of the daytime emigrations that we observed (we had no data on sky conditions for one encounter). Of the 10 diurnal emigrations for which we had data on time since last rainfall, rain had fallen the previous night (potentially disrupting a nocturnal emigration) on six occasions.

Discussion

Emigrations play a critical role by providing army ant colonies access to new foraging grounds, and they determine spacing among colonies (Schneirla, 1971; Teles da Silva, 1977; Franks & Fletcher, 1983). Long-term observations of *E. burchellii* colonies,

Table 1. Numbers of army ant emigration columns encountered at four Neotropical sites.

Army ant species	Systematic trail walk encounters					Opportunistic encounters (BCI–Tiputini, respectively)
	BCI	La Selva	Sta. Maria	Tiputini	Total	
Eciton burchellii	–	2	–	–	2	8–3
Eciton dulcium	1	–	–	–	1	4–0
Eciton hamatum	4	3	–	1	8	–
Eciton lucanoides	–	1	–	–	1	0–1
Eciton mexicanum	1	–	1	2	4	2–0
Eciton rapax	–	–	–	3	3	–
Eciton vagans	–	1	–	–	1	–
Labidus coecus	–	–	3	–	3	–
Labidus praedator	1	–	–	1	2	–
Neivamyrmex cristatus	–	–	–	–	–	0–2
Neivamyrmex gibbatus	–	–	1	1	2	–
Neivamrymex MEK-001	–	–	–	–	–	0–1
Neivamyrmex unk	–	–	–	–	–	0–1
Nomamyrmex esenbeckii	–	–	1	–	1	1–0
Nomamyrmex hartigii	–	–	1	–	1	–
Site totals – no. encounters (no. species)	7 (4; 6*)	7 (4)	7 (5)	8 (5; 9*)		

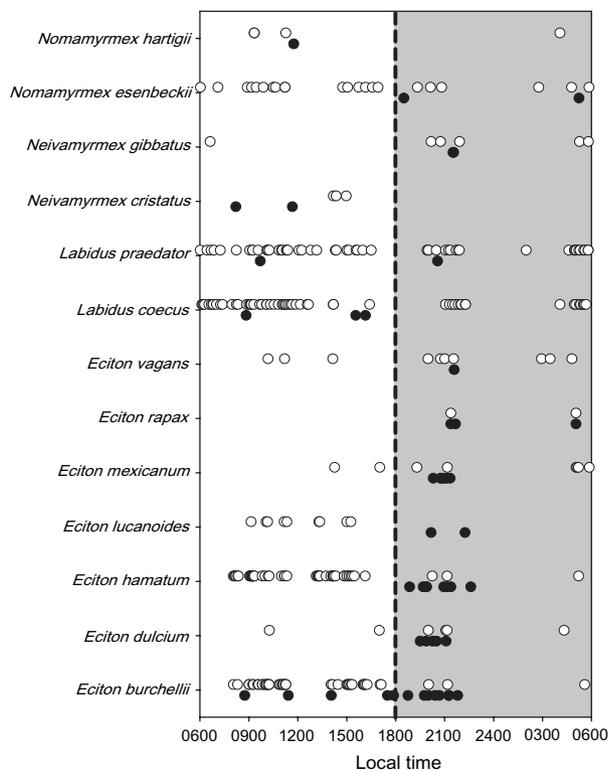*Includes species from opportunistic encounters.

Fig. 2. Time lines indicating time of day of encounters of army ant raid (open symbols) and emigration columns (filled symbols). Dashed vertical line indicates approximate separation of daylight (clear background) from night-time (shaded background) observations.

and data from a few other army ant species, suggest that raids and emigrations are adaptively oriented in space, to reduce rates of revisiting recently exploited patches of forest, and possibly to avoid foraging raid overlap with conspecific colonies (Franks & Fletcher, 1983; Schöning *et al.*, 2005). Some army ants apparently orient their emigration directions relative to their own previous activity, but the importance of intra- and inter-specific colony interactions are less well known (Franks & Fletcher, 1983; Schöning *et al.*, 2005). Anecdotal accounts suggest that some Neotropical *Eciton* exhibit mutual repulsion when foraging parties meet, but whether this influences emigration behaviour is unknown (Swartz, 1997; Willson, 2003). However, emigrations are potentially costly to army ant colonies. Respirometry studies of *Eciton hamatum* showed that the total energy expended on an emigration is approximately four times the energy expended on a 6 h foraging raid, and an emigration does not yield energy intake (Bartholomew *et al.*, 1988).

One of the most striking patterns to emerge from our analysis of army ant community-wide activity, is that both army ant raids and emigrations occur throughout the day. Although some species raid more often in daylight hours, many are active day and night, or only at night. Similar species differences are evident in the distribution of diel timing of emigrations. Summed across the local army ant community, the leaf litter and soil surface of Neotropical wet forests are crossed by army ant raid and emigration columns

throughout the diel cycle. Daylight emigrations were not unusual: a quarter of the emigrations that were observed were in daylight hours. Although our encounter sample sizes were small, our data suggest that diurnal emigration may be a relatively common occurrence for some species.

Daytime emigrations occurred at three of the four study sites and were not restricted to days with overcast sky conditions. Furthermore, not all of the diurnal emigrations could be accounted for by heavy rains disrupting nocturnal bivouac moves the previous night. The several observations of diurnal emigrations by *E. burchellii* at Tiputini are of great interest, because daylight emigration by this species is rarely observed at BCI where most of the previous data have been collected (S. Powell, personal observation). Whether this difference has evolved among populations, or is caused by site differences in biotic or abiotic ecological factors, is unknown. Diurnal emigrations may be more likely to occur during *E. burchellii* colony fission (swarming) events (Nigel Franks, personal communication).

An important but unresolved question is what proximate factors induce the onset of emigration, or the shift from raiding to emigration on a given day. Schneirla (1971) asserted that light was critical to onset of both raiding (rising light) and emigration (falling light) in *E. burchellii*, but did not test this hypothesis directly. However, recent experiments on *E. burchellii* foraging behaviour suggest that although these ants are highly sensitive to changes in temperature, they may not respond to changes in light intensity (Meisel, 2004, 2006). The role of light levels in governing army ant raiding and emigration behaviour, has yet to be critically tested (Gotwald, 1995). Subtle changes in temperature, relative humidity, and intrinsic (circadian) rhythms could each also play a role. Experiments by Topoff and Mirenda (1980) showed that nutritional state could affect the probability of emigration: well-fed colonies were less likely to emigrate on a given day.

Although diurnal emigrations are not rare, many species apparently emigrate largely, or always, at night. Several hypotheses have been advanced to explain the occurrence of nocturnal emigration. Abiotic stresses on army ant brood, particularly larvae, may be reduced at night. Most emigrations that were seen in our systematic sampling occurred during cooler night-time periods, but further temperature variation within time blocks did not predict emigration encounters. Army ant brood are held within homeostatically controlled bivouacs, where temperature and humidity are actively regulated by the workers (Jackson, 1957; Schneirla, 1971; Franks, 1989). Desiccation or wide temperature swings may disrupt brood development, and exposure to nocturnal ambient conditions during emigrations may involve less risk to brood. Biotic factors may also be relevant. Predation pressure on brood by visually hunting predators such as birds, and attacks by highly visual parasites such as phorid flies, may be reduced at night. Spotted ant birds (*Hylophylax naevioides*) kleptoparasitise large prey larvae from army ant foraging columns, and black-faced ant thrushes (*Formicarius analis*) are suspected of doing so as well (Swartz, 1997; S. Powell, pers. obs.). A diurnal emigration column with mature larvae would likely represent a conspicuous target to these birds. Moreover, each colony has a single, large queen that if lost, would result in colony demise.

Two significant site differences in army ant emigration activity are notable. The first is the apparent diel shift of emigration activity toward later in the night (AM dark phase) at Sta. Maria. Differences in species abundance could cause such site differences, to the extent that species differ in their typical diel patterns of emigration. Sta. Maria is also higher in elevation than the other sites, raising the possibility that the elevational changes in temperature and other abiotic factors could affect patterns of emigration behaviour. The second site difference is the high overall rate of emigrations at Tiputini, which is especially salient, because raid rates were intermediate at this site (O'Donnell *et al.*, 2007). There are at least two behavioural patterns that could account for this difference: emigration columns could be longer at this site, and emigrations could be more frequent. Even in species that have a well-defined nomadic phase, like *E. burchellii*, some emigration days are skipped in most nomadic cycles (Schneirla, 1971; Franks & Bossert, 1983). In Tiputini, the frequency of these skipped days may be lower, resulting in higher emigration activity overall.

Acknowledgements

References

Bartholomew, G.A., Lighton, J.B. & Feener, D.H.Jr (1988) Energetics of trail running, load carriage, and emigration in the column-raiding army ant *Eciton hamatum*. *Physiological Zoology*, **61**, 57–68.

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 of the United States of America*, **100**, 6575–6579.

Franks, N.R. (1982) A new method of censusing animal populations: the number of *Eciton burchelli* army ant colonies on Barro Colorado Island, Panama. *Oecologia*, **52**, 266–268.

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* (ed. by E.G.J. Leigh, A. S. Rand and D. M. Windsor), pp. 389–396. Smithsonian Institution Press, Washington, DC.

Franks, N.R. (1989) Thermoregulation in army ant bivouacs. *Physiological Entomology*, **14**, 397–404.

Franks, N.R. & Bossert, W.H. (1983) Swarm raiding army ants and the patchiness and diversity of a tropical leaf litter ant community. *The Tropical Rain Forest, British Ecological Society Symposium* (ed. by S. L. Sutton, A. C. Chadwick and T. C. Whitmore), pp. 151–163. Blackwell, Oxford.

Franks, N R. & 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, New York.

Jackson, W.B. (1957) Microclimatic patterns in the army ant bivouac. *Ecology*, **38**, 276–285.

Kaspari, M. (1996) Litter ant patchiness at the 1-m^2 scale: disturbance dynamics in three Neotropical forests. *Oecologia*, **107**, 265–273.

Kronauer, D.J.C., Rodriguez Ponce, E.R., Lattke, J.E. & Boomsma, J.J. (2007) Six week in the life of a reproducing army ant colony: male parentage and colony behaviour. *Insectes Soiaux*, **54**, 118–123.

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., Hespenheide, H.A. & Hartshorn, G.S. (1994) *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press Chicago, Illinois.

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, Madison, Wisconsin.

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

Mirenda, J.T., Eakins, D.G., Gravelle, K. & 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. & 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 abundance. *Journal of Animal Ecology*, **76**, 580–589.

Powell, S. & Baker, B. (2008) Os grandes predadores dos neotrópicos: comportamento, dieta e impacto das formigas de correição (Ecitoninae). *Insetos Sociais da Biologia à Aplicação* (ed. by E. Ferreira Vilela, I. A. dos Santos, J.E. Serrão, J.H. Schoereder, J. Lino-Neto and L. A. de O. Campos), pp. 18–37. Universidade Federal de Viçosa, Viçosa, Brazil.

Rettenmeyer, C.W. (1963) Behavioural studies of army ants. *University of Kansas Science Bulletin*, **9**, 281–465.

Schneirla, T.C. (1945) The army-ant behavior pattern: nomad–statary relations in the swarmers and the problem of migration. *Biological Bulletin*, **88**, 166–193.

Schneirla, T.C. (1971) *Army Ants: A Study in Social Organization*. Freeman, San Francisco, California.

Schöning, C., Njagi, W.M. & Franks, N.R. (2005) Temporal and spatial patterns in the emigrations of the army ant *Dorylus (Anomma) molestus* in the montane forest of Kenya. *Ecological Entomology*, **30**, 532–540.

Swartz, M.B. (1997) *Behavioral and population ecology of the army ant* Eciton burchelli *and ant-following birds*. PhD thesis, University of Texas–Austin, Austin, Texas.

Teles da Silva, M. (1977) Behaviour of the army ant *Eciton burchelli* Westwood (Hymenoptera: Formicidae) in the Belem region. I. Nomadic–statary cycles. *Animal Behaviour*, **25**, 910–923.

Topoff, H. & Mirenda, J. (1980) Army ants on the move: relation between food supply and emigration frequency. *Science*, **207**, 1099–1100.

Topoff, H. Mirenda, J., Droual, R. & Herrick, S. (1980) Behavioral ecology of mass recruitment in the army ant *Neivamyrmex nigrescens*. *Animal Behaviour*, **28**, 779–789.

Vidal-Riggs, J.M. & Chaves-Campos, J. (2008) Method review: estimation of colony densities of the army ant *Eciton burchellii* in Costa Rica. *Biotropica*, **40**, 259–262.

Willson, S.K. (2003) *Army ants and obligate ant-following birds: a study of ecology, spatial movement patterns and behavior in Amazonian Peru*. PhD thesis, University of Missouri, Columbia, Missouri.

Wilson, E.O. (1958) The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution*, **12**, 24–36.