

Diurnal and nocturnal foraging specialisation in Neotropical army ants

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Abstract. 1. Temporal segregation of species' activity periods may lessen interspecific competition.

2. We tested for temporal segregation among Neotropical army ants (Formicidae: Dorylinae). Co-occurring species overlap on prey resources, and regular colony movements and long-distance raiding increase interspecific interference.

3. We hypothesised interspecific competition selects for temporal separation of species' raid periods into diurnal versus nocturnal activity. We predicted species would differ significantly in their timing of foraging. We further predicted timing would differ among congeners because close relatives likely overlap in resource needs.

4. Trail walk encounter rates were used to estimate species' diurnal versus nocturnal foraging activity at four Neotropical sites.

5. Army ant species differed significantly in foraging times. There were significantly diurnal and nocturnal specialists; some species foraged at similar rates day and night. Two genera (*Eciton* and *Neivamyrmex*) included both diurnal and nocturnal specialists. Relative eye size (a morphological indicator of above-ground activity) was positively associated with diel foraging specialisation (both diurnal and nocturnal).

6. Temporal separation of foraging times may play a role in allowing Neotropical army ant species to occupy the same habitat. Diel specialisation may be a common mechanism for species coexistence in tropical forests where season-based phenological changes are often moderated.

Key words. Central America, Diel cycle, Formicidae, South America, temporal partitioning.

Introduction

Temporal segregation of activity periods may promote the geographic coexistence of multiple species that exploit similar resources (Kronfeld-Schor & Dayan, 2003).

In temperate habitats, phenological partitioning, i.e., species replacing each other seasonally, may contribute to local species richness among potential competitors (Sowig & Wassmer, 1994; Shuter *et al.*, 2012; Wagg *et al.*, 2017). Phenological cues and seasonal variation are weaker in some tropical habitats, particularly in wet lowland forests, reducing opportunities for

phenological partitioning. We suggest diel partitioning of activity among species, for example between diurnal and nocturnal guilds, may promote high species richness in the tropics.

Neotropical army ants are strictly carnivorous top predators (Schneirla, 1971; Gotwald, 1995; Rettenmeyer *et al.*, 1983; Anderson *et al.*, 2012) that share several unusual features of foraging behaviour. These include mass raiding and recruitment to prey and specialisation on consuming the brood of other social insects (Rettenmeyer *et al.*, 1983; Kronauer, 2009; Powell, 2011). Despite their shared behavioural ecology, a dozen or more species of army ants typically co-occur at forested Neotropical sites (O'Donnell *et al.*, 2007, 2009). Many army ant species target different genera or even species of ants as prey, but there is some diet overlap among sympatric species, suggesting army ants could experience interspecific exploitation

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competition for prey resources (Rettenmeyer *et al.*, 1983; Otis *et al.*, 1986; Kaspari *et al.*, 2011; Hoenle *et al.*, 2019; Manubay & Powell, 2020).

Spatial habitat partitioning can be an important component of ant community composition and may promote regional ant species richness (Albrecht & Gotelli, 2001; Kneitel & Chase, 2004; Yusa *et al.*, 2018), but spatial segregation is challenging for army ant species. Army ant colonies are mobile, regularly emigrating among temporary nests sites (Kronauer, 2009; O'Donnell *et al.*, 2009; Soare *et al.*, 2020). Furthermore, army ant colonies send out raid parties almost daily which move in directional columns across linear distances of 100 m or more (Swartz, 1997; Willson *et al.*, 2011). In addition to potential food resource competition, colonies whose raids collide can incur costs via interference. Interspecific raid encounters can lead to foraging column redirection, workers engaged in ritualised avoidance displays instead of foraging, and in some cases deadly battles among workers (Swartz, 1997; Willson *et al.*, 2011; Baudier & Pavlic, in review).

Temporal separation of activity periods may be an alternative to spatial segregation for reducing negative interspecific interactions among mobile animals like army ants. We hypothesised that army ant species benefit by raiding at different times of the day and we predicted sympatric army ants would specialise by foraging diurnally or nocturnally, as seen in other ant communities (Narendra *et al.*, 2016, 2017; Grevé *et al.*, 2019). Army ants are known to forage throughout the diel cycle, and there is evidence that species differ by foraging more often in daylight or alternatively under cover of darkness (O'Donnell *et al.*, 2007, 2009; Hoenle *et al.*, 2019). To test for diel segregation of raid activity we analysed quantitative data on army ant raid frequencies that were collected at different phases of the diel cycle (diurnal vs. nocturnal) using a standardised trail walk protocol (O'Donnell *et al.*, 2007, 2009). We collected these data at four Neotropical forested sites, with sampling effort divided between daylight and nighttime hours at each site. We used per-kilometre rates of encountering diurnal and nocturnal foraging raids to test whether species were specialised on daylight or nighttime foraging. Analyses of community-level patterns of raiding, site differences in species diversity, and emigration activity from this data set were published previously (O'Donnell *et al.*, 2007, 2009).

Neotropical army ants vary widely in their degree of above-versus under-ground foraging and nesting activity (Baudier *et al.*, 2015, 2018). We asked whether species differences in relative above-ground activity were associated with specialisation on foraging during daylight or nighttime hours. We used relative eye size (RESI: Baudier *et al.*, 2015, 2018) as an index of species' relative above-ground versus subterranean behaviour. RESI is a ratio of eye size to head capsule size, measured on small-bodied workers. RESI corresponds to measures of above-ground raiding and nesting activity (Baudier *et al.*, 2015, 2018). Worker army ant eyes (when present; some subterranean species are eyeless) comprise a single external facet and cannot form images (O'Donnell *et al.*, 2018).

Understanding army ant diel specialisation is relevant to tropical ecology because army ants function as keystone top predators (Franks & Bossert, 1983; Boswell *et al.*, 1998;

Gotwald, 1995; Meisel, 2001; Kaspari & O'Donnell 2003). Shifts in top predator activity timing can affect diel activity patterns of other community members (Cunningham *et al.*, 2019). Diel specialisation also has important implications for the biology of army ant species. Diel (diurnal versus nocturnal) timing of foraging activity may further differentiate army ant species physiology, with implications for species responses to directional climate change (Garcia-Robledo *et al.*, 2018).

Materials and methods

Diel time blocks for sampling raid activity

Sampling trail walks began during four different time blocks. The range of start times for each time block was: AM daylight (08.00–10.30 hours), PM daylight (12.30–15.40 hours), PM dark (19.15–20.15 hours), and AM dark (02.00–04.55 hours) (O'Donnell *et al.*, 2007, 2009). Raid column observations were categorised as occurring either when the sun was above the horizon (daytime raids) or after the sun had set (nighttime raids) in our analysis.

Study sites and sampling dates

For each site, we list latitude/longitude coordinates, elevation range of army ant sampling, Holdridge life zones (Holdridge, 1966), and dates of sampling. (i) La Selva Biological Station, Costa Rica. 10°26'N, 83°59'W. 40–130 m asl. Tropical Wet Forest. 11 June to 4 August 2003. (ii) Barro Colorado Island (BCI) Research Station, Panama. 9°09'N, 79°50'W. 60–190 m asl. Tropical Moist Forest. 20 July to 9 September 2003. (iii) Santa Maria Valley, Henri Pittier National Park, Venezuela. 10°22'N, 67°49'W. 530–840 m asl. Premontane Humid Forest. 1 August to 2 September 2003. (iv) Tiputini Biodiversity Research Station, Ecuador. 0°38'S, 76°08'W, 190–230 m asl. Tropical Moist Forest. 25 September to 16 October 2003.

Trail walk protocols

We walked pre-selected trails to sample army ant raid activity (O'Donnell *et al.*, 2007). We chose trails of 1.0–4.7 km in length and walked them repeatedly to search for army ants. Walking trails is effective for detecting army ant raids; subterranean species often travel above-ground across established human trails, possibly in response to local soil compaction (Rettenmeyer, 1963; Franks, 1982; O'Donnell *et al.*, 2007; Vidal-Riggs & Chaves-Campos, 2008). Army ant raid columns are often highly directional and raids can travel linear distances of over 100 meters from the bivouac. The unbroken raid columns of ants are likely to intersect trails walked for sampling (Rettenmeyer, 1963; Schneirla, 1971; Franks, 1985). We searched for army ant foraging activity while walking the selected trails at speeds of approximately 1 km h⁻¹. We illuminated the path with headlamps and/or flashlights when working at night. We conducted a maximum of two walks per site per calendar day.

A small number of trail walks at each site (\leq five per site) were cancelled or shortened during periods of heavy rainfall. During trail walks, we continually scanned the ground for army ant activity. We recorded only army ant raid columns that contacted the sampling trail. We identified a column as a raid (rather than an emigration column: O'Donnell *et al.*, 2009) if workers were carrying prey items and none were seen carrying army ant brood (larvae or pupae), and no callow (pale, newly emerged) workers were present. Some colony emigrations may have been mistaken for raid columns because ants at the beginning of emigration columns carry prey and do not always carry brood (Schneirla, 1971). When we encountered an army ant raid we recorded time to the nearest minute, and we stopped for approximately 10 min to collect data and voucher specimens into 70% ethanol.

We conducted 82 diurnal trail walks totalling 234.1 km, and 40 nocturnal trail walks totalling 117.9 km. Sampling efforts at each site were as follows. BCI: diurnal 21 walks, 73.5 km; nocturnal 14 walks, 46.3 km; La Selva: diurnal 19 walks, 86.1 km; nocturnal 6 walks, 31.8 km; Sta. Maria: diurnal 25 walks, 35.5 km; nocturnal 16 walks, 27.7 km; Tiputini: diurnal 17 walks, 43.3 km; nocturnal 4 walks, 11.4 km.

We used the per-walk frequency of encounters of army ant raids during each trail walk as our measure of above ground foraging activity for each species. We treated each trail walk at a site as an independent data point, and we accounted for the possible effects of variation in walk distances in our analyses (see below). If we encountered multiple raid columns of a single species within 50 m linear distance of the nearest column of the same species on a single walk, these columns were assumed to belong to the same colony and were treated as one encounter.

Data analyses

Most statistical tests were performed using SPSS version 26 software. We used Generalised Linear Models to test for statistical effects of covariates (site, diel timing) on frequencies of encountering army ant raids. We modelled the error structure of the models as a negative binomial with a log link, which is appropriate for count data with high variances, for example, when zeros predominate the observations (Lawless, 1987). We treated trail walks as independent data points, using the frequency (count data) of encounter of raid columns of a given species on a walk as the response variable. Because trail walks differed in length both within and among sites, we used the distance traversed in each walk (to the nearest 50 m) as a scale-weight variable to account for the effects of these differences in sampling effort. Violin plots of data distributions were produced in Graphpad Prism version is 8.3.0 with data smoothing set to heavy. Data on trail walk encounters are presented in Supplemental information (File S1).

Site differences

We first performed a Generalised Linear Models test to compare overall raid frequencies in the daylight versus nighttime trail walk samples. We tested whether sites differed in raid

frequencies, then tested whether diurnal and nocturnal raid frequencies differed (summed across all army ant species). We also tested whether sites differed in their proportions of diurnal versus nocturnal raid activity, summed across army ant species, by using the site * diel timing interaction term.

Species differences

We tested for statistical effects of covariates (site, diel timing) on each army ant species' raid encounter frequencies. We included only the relatively common species, those observed raiding five or more times, in these analyses ($n = 10$ species). All common species except two *Neivamyrmex* species were observed at multiple sites. For each species, we tested per-walk raid frequency as the response variable. The model included geographical study site (except when species were seen at one site) and time block (diurnal vs. nocturnal) as predictor variables. We tested whether significant differences in encounter frequencies were biased toward daytime or nighttime activity for each species.

We analysed the association between species' above-ground activity (indexed by RESI) and the diel specialisation index using phylogenetic generalised least-squares regression (PGLS; Rohlf, 2001). PGLS tests for relationships among species-level traits while estimating and accounting for the effects of species relatedness (phylogeny) on the traits. To quantify each species' degree of diel specialisation, we calculated an index of diurnal activity based on the overall mean per kilometre rate of diurnal and nocturnal raid encounters across all sites where the species occurred in our sample:

$$\text{Diurnal activity index} = \frac{(\text{daytime rate})}{(\text{daytime rate} + \text{nighttime rate})} \quad (1)$$

This index ranges from 0 (for strictly nocturnal species) to 1 (for strictly diurnal species) and is independent of variation in overall encounter rates; if daytime and nighttime rates are equal for a species, the index value is 0.5. To quantify diel specialisation (regardless of whether a species was diurnally or nocturnally active), we developed a diel specialisation index:

$$\text{Diel specialisation index} = \text{absolute value of} \\ (\text{diurnal activity index} - 0.5) \quad (2)$$

The diel specialisation index ranges from 0 (for species with equal daytime and nighttime foraging rates) to 0.5 (for fully diurnal or nocturnal species).

To test whether above-ground activity was associated with greater diel specialisation (diurnal or nocturnal), we used a previously published morphological indicator of species relative degree of above-ground activity (RESI: relative eye-size index; Baudier *et al.*, 2015, 2018; there were no RESI data available for *Neivamyrmex emersoni* so this species was excluded from the analysis). We used a *T*-test to assess whether RESI differed between significantly diurnal and nocturnal specialist species.

The phylogeny and branch lengths (estimated divergence times in millions of years ago (MYA)) for the subject species

Table 1. Army ant species per-kilometer rates of raid encounters for the 10 most frequently-observed species during standardised trail-walk samples at four Neotropical sites, separated by phase of the diel cycle (top- diurnal, bottom- nocturnal).

Site	Diel period	Species									
		<i>E. h.</i>	<i>E. b.</i>	<i>Ne. p.</i>	<i>No. e.</i>	<i>L. c.</i>	<i>L. p.</i>	<i>E. a.</i>	<i>E. v.</i>	<i>Ne. e.</i>	<i>Ne. g.</i>
BCI	Day	0.29	0.01	0.04	0.03	0.10	0.12	0.01			
La Selva	Day	0.27	0.35	0.10	0.10	0.05	0.02	0.01	0.03		
Sta. Maria	Day		0.14	0.20	0.34	0.51	0.42				
Tipu	Day	0.18	0.09		0.05	0.05	0.05				
BCI	Night	0.02			0.02	0.04	0.11	0.11			
La Selva	Night	0.03	0.06	0.00					0.03		
Sta. Maria	Night				0.18	0.90	0.69	0.07	0.22	0.18	0.22
Tipu	Night	0.09	0.09			0.09	0.18				

Open columns: significantly diurnal species; Light gray columns: species with no significant diel bias; Dark gray columns: significantly nocturnal species. Only cell values with observed raid encounters are filled in for clarity; empty cells represent zeros.

Study sites: BCI = Barro Colorado Island, Panama; La Selva = La Selva Biological station, Costa Rica; Sta. Maria = Henri Pittier National Park, Venezuela; Tipu = Tiputini Biodiversity Station, Ecuador.

Army ant species: *E. h.*, *Eciton hamatum*; *E. b.*, *Eciton burchellii*; *Ne. p.*, *Neivamyrmex pilosus*; *No. e.*, *Nomamyrmex esenbeckii*; *L. c.*, *Labidus coecus*; *L. p.*, *Labidus praedator*; *E. m.*, *Eciton mexicanum*; *E. v.*, *Eciton vagans*; *Ne. e.*, *Neivamyrmex emersoni*; *Ne. g.*, *Neivamyrmex gibbatus*.

were obtained from Brady *et al.* (2014), Winston *et al.* (2016) and Borowiec (2019). When a branch length was not available for a given node, we assigned the divergence event to the halfway point between the preceding node and the next dated node or the present (Baudier *et al.*, 2018). The PGLS analysis was run in R version 4.0.2 using the CAPER package (Comparative Analyses of Phylogenetics and Evolution: <https://cran.r-project.org/package=caper>). The phylogeny used in the analyses is presented in Supplemental information (File S2).

Results

Overall site differences and diel patterns of raid activity

Both diurnal and nocturnal raids were observed at all sites (Table 1; Fig. 1). Summed across all army ant species, sites differed significantly in raid encounter frequencies (Fig. 1; Wald chi-square = 24.8, df = 3, $p < 0.001$). Trail walk encounter rates with army ant raids were significantly higher at night than during the day (Wald chi-square = 6.48, df = 1, $p = 0.011$), but sites differed in the relative frequency of diurnal versus nocturnal raids (Fig. 1; Site * diel period interaction term Wald chi-square = 36.9, df = 3, $p < 0.001$).

Species differences in diurnal versus nocturnal foraging activity

Significantly diurnal and non-specialised species were observed at all sites, and significantly nocturnal species were observed at all sites except Tiputini (Table 1). Three species were significantly more active foraging in daylight observations (Fig. 2; *Eciton hamatum*: Wald chi-square = 32.4, df = 1, $p < 0.001$; *Eciton burchellii*: Wald chi-square = 16.2, df = 1, $p < 0.001$; *Neivamyrmex pilosus*: Wald chi-square = 11.9, df = 1, $p < 0.005$). Four species were significantly more active foraging in nighttime observations (Fig. 2; *Eciton mexicanum*:

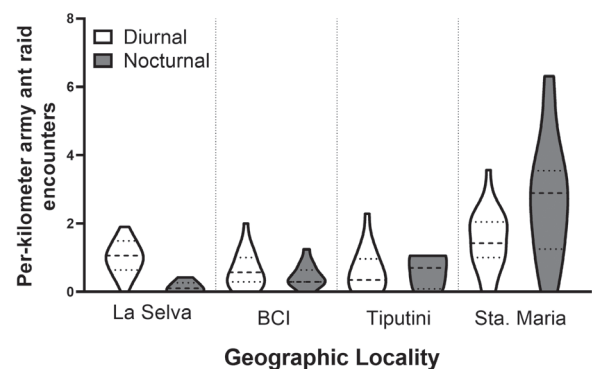


Fig 1. Violin plot showing distributions of per-kilometer rates of encountering army ant raids during diurnal and nocturnal standardised trail walks at four Neotropical forested sites. La Selva: La Selva Biological Station, Costa Rica; BCI: Barro Colorado Island, Panama; Tiputini: Tiputini Biodiversity Station, Ecuador; Sta. Maria: Santa Maria Valley, Henri Pittier National Park, Venezuela. Dashed line inside shapes indicates median, dotted lines indicate quartiles, and limits of the shape indicate the range of data values. Width of the plotted shapes indicates the number of data points in that range of values (with smoothing).

Wald chi-square = 11.9, df = 1, $p < 0.005$; *Eciton vagans*: Wald chi-square = 4.4, df = 1, $p = 0.036$; *N. emersoni*: Wald chi-square = 8.4, df = 1, $p < 0.005$; *N. gibbatus*: Wald chi-square = 6.6, df = 1, $p = 0.010$). Three species showed no significant difference in diurnal vs. nocturnal foraging encounters (Fig. 2; *Nomamyrmex esenbeckii*: Wald chi-square = 0.21, df = 1, $p = 0.649$; *Labidus praedator*: Wald chi-square = 2.4, df = 1, $p = 0.118$; *Labidus coecus*: Wald chi-square = 0.001, df = 1, $p = 0.980$). The lack of day/night difference in these three cases was not due to low statistical power: these three species were among the most abundant in our samples and they were observed at three or four sites; their overall encounter frequencies were higher than many of the species showing significant day/night differences (Fig. 2).

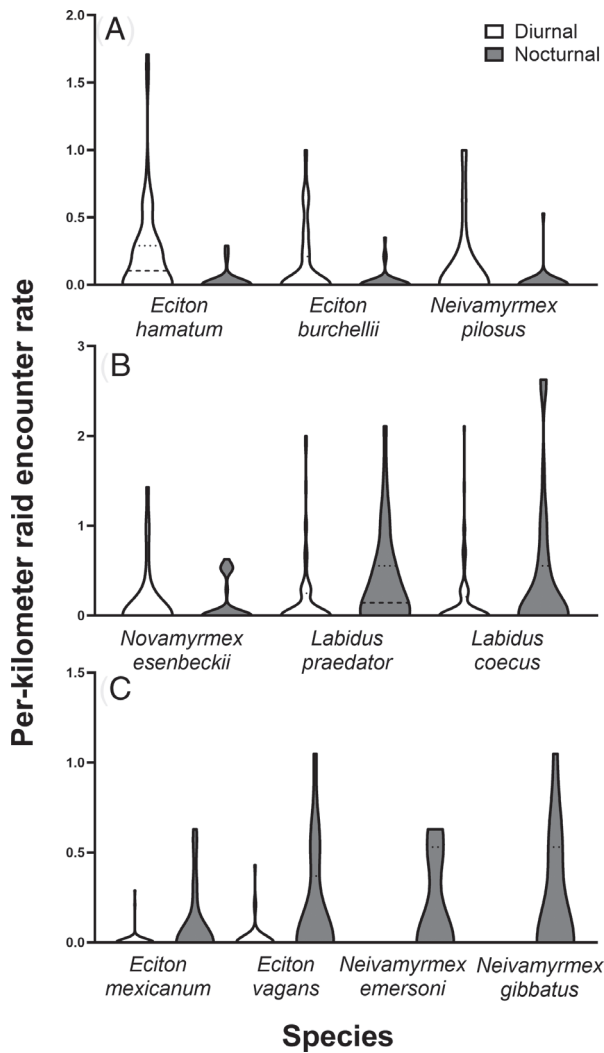


Fig 2. Violin plot showing diurnal and nocturnal raid rates (per-kilometer raid encounters) for the 10 most common species of army ants sampled at four Neotropical forest sites. Panel A: Significantly specialised diurnal species. Panel B: Species that did not differ significantly in diurnal versus nocturnal foraging. Panel C: Significantly specialised nocturnal species. Dashed line inside shapes indicates median, dotted lines indicate quartiles, and limits of the shape indicate the range of data values. Width of the plotted shapes indicates the number of data points in that range of values (with smoothing).

Phylogenetic effects

Diel specialisation (both diurnal and nocturnal) was strongly positively associated with above-ground activity after accounting for phylogenetic effects (Fig. 3; PGLS regression $R^2 = 0.74$, $F_{1,7} = 19.9$, $p < 0.005$). It is important to note that RESI is an index of above-ground activity rather than an index of diurnal foraging. For the six species that specialised significantly on foraging diurnally (three species) or nocturnally (three species with RESI values; Fig. 1), RESI did not differ significantly between diurnal and nocturnal species (Fig. 3; T -test $t = -0.85$, $df = 4$, $p = 0.442$).

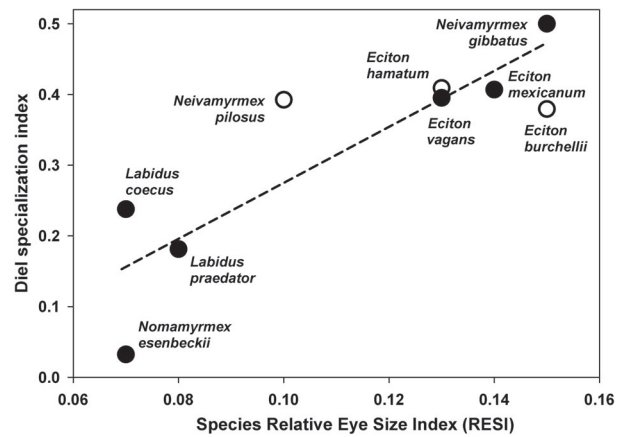


Fig 3. Relationship between a morphological index of above-ground activity (RESI) and diel foraging activity specialisation (diurnal or nocturnal) for nine army ant species sampled in the Neotropics. Dashed line represents best-fit relationship from phylogenetic generalised least-squares regression analysis. Symbol shading represents diel biases in foraging activity (white: significantly diurnal species; black: significantly nocturnal species; gray: species with similar day and night foraging activity).

Discussion

Evidence for diel separation and site differences

Our data support the hypothesis that army ant species diverged in diel timing of foraging behaviour, with some species specializing on diurnal foraging and others on nocturnal foraging. There are also species that divide foraging effort across the diel cycle. Army ant foraging occurred day and night at all sites, although sites differed in both overall army ant foraging frequencies and in the relative diurnal versus nocturnal raid frequencies. The site differences may be driven in part by different species compositions and relative species abundances among the sites (O'Donnell *et al.*, 2007).

Evolution of diel specialisation

Although Neotropical army ant species specialise on prey taxa (mainly other species of ants), avoidance of exploitation competition could favour interspecific temporal separation of foraging across the diel cycle when species overlap partially on the same prey taxa. However, reduction of interference competition is expected to play a stronger role than exploitation competition in the evolution of temporal specialisation by foragers (Carothers & Jaksic, 1984), and we suggest army ants are particularly likely to be impacted by and respond to foraging interference. Regular long-distance (100 linear m or more) emigrations among nest sites, and similarly long and roughly linear foraging columns, both elevate the probability that army ant raids will encounter other army ant species while foraging. Although cross-species behavioural responses to foreign raids vary in intensity, they are likely always costly to both participants in an encounter. Species-level partitioning of the diel cycle could ameliorate these effects at a given site.

If diel specialisation is an evolved trait, an important remaining question is what directions of behavioural change have occurred: nocturnal to diurnal, or vice versa. Specialised diurnal or nocturnal foraging likely involve distinct costs and benefits. For example, shifts to diurnal foraging could provide access to novel prey resources. Surface active, swarm-raiding army ant raids drive out potential prey items that flee before them, but diurnal army ant raids can be attended by birds and other vertebrates that kleptoparasitise potential prey from the ants (Willis & Oniki, 1978; Wrege *et al.*, 2005; O'Donnell *et al.*, 2010). Because avian kleptoparasites are strictly diurnal, nocturnal raids could reduce the birds' negative effects on prey capture rates, imposing a special cost on diurnal foraging. Diel patterns of prey activity may affect the probability of their discovery by army ants. At least some army ants appear to be heavily reliant upon prey movement for successful detections and capture; some army ant prey can escape detection by freezing until a raid passes (Rettenmeyer, 1963; Gotwald, 1995; Dejean *et al.*, 2014).

Foraging raid behaviour also interacts with army ant colony needs to emigrate among temporary nest sites during part of the colony cycle (Schneirla, 1971). Although some army ant species occasionally emigrate in daylight, nocturnal emigrations predominate (O'Donnell *et al.*, 2009). Diurnal emigrations may be disfavoured because they place the brood and queen at risk to visually hunting vertebrates, and/or because high diurnal temperatures and low humidity physiologically stress the brood. Because emigrations can take many hours to complete (Rettenmeyer, 1963; Franks, 1985), emigrations may preclude or restrict nocturnal foraging activity.

Above-ground activity and diel specialisation

There was an association between above-ground activity and diel raid specialisation: both significantly diurnal and significantly nocturnal species were more likely to be active above-ground. Two genera, *Eciton* and *Neivamyrmex*, included both diurnal and nocturnal above-ground active species. The ability to raid day and night could be favoured if subterranean species are buffered from ambient abiotic variation, effectively rendering day/night differences irrelevant for these species. Other factors could contribute to this difference. For example, the *Labidus* and *Nomamyrmex* species we sampled may have relatively large colony sizes (Rettenmeyer, 1963; Beckers *et al.*, 1989; Barth *et al.*, 2014) that engage in long-lasting emigrations or raids. This may preclude them from completing either activity within a single diurnal or nocturnal cycle. One documented raid of *N. esenbeckii* against a mature colony of leaf-cutting ants resulted in over 35 h of continuous prey retrieval (Powell & Clark, 2004), while Rettenmeyer (1963) documented a complete emigration of the same species that spanned approximately 20 h.

Implications of our findings

Diel timing of raid activity has implications for the thermal biology of army ant species. Army ant workers walk and do

not cluster when raiding, so workers do not thermoregulate socially outside the nest. Tropical ants in the body size range of Neotropical army ant workers have little capacity to thermoregulate individually moving across typical temperature differentials encountered on the forest floor (for example, sun vs. shade). These ant workers reach thermal equilibrium in <10 s (Kaspari *et al.*, 2015; S. O'D. unpub. data). Army ant workers outside of their bivouacs are poikilotherms, operating at ambient temperatures nearly continuously. Behavioural and physiology data suggest the partially subterranean activity of some army ant species may buffer workers from ambient environmental extremes; conversely, above-ground active species are exposed to local ambient extremes (Baudier *et al.*, 2015, 2018). Diurnally foraging species are exposed to greater extremes of both high temperature and low humidity than their nocturnal counterparts, suggesting that diel specialisation could be relevant to understanding army ant thermal ecology.

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Data availability statement

Data on army ant trail walk encounters as analysed and presented in this paper are openly available in the paper's Supporting information as File S1 (spreadsheet).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Data on diel timing of army ant foraging column encounters from four Neotropical sites.

File S2. Phylogeny (Newick format) used for PGLS species comparative analysis of army ant above-ground activity and diel foraging specialisation.

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