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Elevational and geographic variation in army ant swarm raid rates

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Abstract Geographic and elevational variation in the local abundance of swarm-raiding army ants has implications for the population dynamics of their prey, as well as affecting the profitability of army-ant-following behavior for birds. Here, we analyze systematically collected data on *E. burchellii* and *L. praedator* raid rates from geographically and elevationally wide-ranging sites, from lowland to montane forests. We show that raids of each species, and of both species pooled, reach peak densities at intermediate (premontane) elevations. These patterns suggest that army ant swarm raids are relatively abundant in Neotropical montane forests. Therefore, a paucity of ant raids does not explain the absence of obligate ant-following bird species, particularly true antbirds (Thamnophilidae), from montane forests. As army ant raids are relatively common at middle elevations, opportunities exist for other montane bird taxa to exploit army ant raids as a food source.

Keywords Antbirds · *Eciton burchellii* · Ecitoninae · *Labidus praedator*

Introduction

Army ants (Ecitoninae) are a ubiquitous force of predation in Neotropical forest leaf litter (Kaspari and O'Donnell, 2003). The army ant guild at any one site can comprise over 15 species (Rettenmeyer et al., 1983; Quiroz-Robledo et al., 2002; O'Donnell et al., 2007). However, army ant species assemblages vary geographically. Standardized samples of army ant foraging raid rates at four sites found significant geographic differences in army ant species composition, and in the absolute and relative densities of the most abundant army ant species (O'Donnell et al., 2007). Army ant density also varies with elevation (O'Donnell and Kumar, 2006; Kumar and O'Donnell, 2009). Army ant species differ in prey preferences, foraging substrate (i.e., subterranean vs. above ground), and in the diel timing of their raid activity (Rettenmeyer, 1963; Rettenmeyer et al., 1983; Powell and Franks, 2006; O'Donnell et al., 2009). Therefore, geographic variation in army ant species composition and relative abundance will affect the magnitude of predation pressure army ants exert on a given prey taxon.

The surface swarm raids of some army ants, notably *Eciton burchellii* and *Labidus praedator*, have ecological impacts beyond predation because they are attended by a diverse array of birds (Willis, 1966; Willis and Oniki, 1978;

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Meisel, 2004; Willson, 2004). Raid-attending birds cleptoparasitize the ants by consuming large bodied arthropods that flee from the advancing ant swarm (Wrege et al., 2005). Bird species vary in their degree of reliance on army ant raids for food. Some species in the antbird family (Thamnophilidae) are obligate raid attendants, obtaining nearly all of their food at army ant raids (Willson, 2004; Brumfield et al., 2007). Other bird species are opportunistic raid attendants, but some have behavioral specializations for attending ant raids (Meisel, 2004; O’Donnell et al., 2010).

In both Central and South America, obligate army-ant-following birds are restricted to elevations below approximately 1,000 m asl, raising questions about factors limiting the geographic and elevational ranges of obligate antbirds (S. O’D. and A.K., pers. obs.; Willis, 1967; Hilty, 1974; Blake and Loiselle, 2000). There are numerous assertions in the literature that army ant density decreases with elevation and latitude, and that this limits opportunities for birds to attend raids (Willis, 1966; Hilty, 1974; Willis and Oniki, 1978; Dobbs and Martin, 1998; Rios et al., 2008). At extreme latitudes and elevations, this is true-surface raiding army ants do not occur north of approximately 22°N for *L. praedator* and 23.8°N for *E. burchellii* (Watkins, 1976), nor do these ants occur in high elevation forests. It has also been suggested that *L. praedator* ranges to higher elevations than *E. burchellii* when they occur at the same latitude (Hilty, 1974). However, geographic and elevational patterns of the density of surface swarm-raiding army ants have not been systematically quantified.

Here, we summarize data on the density of diurnal army ant swarm raids on the forest floor. Data were collected at several Neotropical sites that varied widely in latitude and elevation. We used these data to test whether swarm raid densities decline with elevation. We also asked whether declines in army ant swarm raid density were congruent with the ranges of obligate antbirds, as would be expected if local swarm raid density determines obligate antbird presence at a given location.

Methods

Trail walk sampling protocol

We quantified *E. burchellii* and *L. praedator* foraging raid activity using trail walk sampling (O’Donnell and Kumar, 2006; O’Donnell et al., 2007; Vidal-Riggs and Chaves-Campos, 2008). We chose trails to walk repeatedly for the purpose of sampling army ant raid activity at each site. We searched for army ant activity while walking trails at speeds of approximately 1 km/h. When we encountered army ants, we collected a sample of several dozen workers and the items they were carrying into 95% EtOH for later identification. We recorded only raid columns that were carrying prey items; army ant columns carrying their own larvae were assumed to represent colony emigrations and were not counted (O’Donnell et al., 2009). The trails we walked were located in primary forest, but some of the trails passed through areas of old second growth forest (>40 years regeneration). The trails ranged from 1.0 to 4.7 km in length. We did not analyze walks in open areas because many raid-attending birds avoid leaving forest cover (Karr, 1982; Laurance et al., 2002). We conducted a maximum of two walks per site per calendar day. We analyzed only trail walks that were conducted completely during daylight hours when birds attend raids. A small number of walks at each site (≤5 per site) were cancelled or shortened during periods of heavy rainfall, when both ant and bird activity typically cease. Pooled across the sample sites, we conducted a total of 193 daytime trail walks totaling 409 km in length (mean 2.1 km/walk).

Sampling locations

For each site, we list latitude/longitude coordinates, elevation range, Holdridge Life Zone (Holdridge, 1966), and dates of trail walk sampling.

La Selva Biological Station, Costa Rica; 10°26′N, 83°59′W; 40–130 m asl; Tropical Wet Forest; 11 June–4 August 2003.
Barro Colorado Island Research Station, Panama; 9°09′N, 79°50′W; 60–190 m asl; Tropical Moist Forest; 20 July–9 September 2003.
Tiputini Biodiversity Research Station, Ecuador; 0°38′S, 76°08′W; 190–230 m asl; Tropical Moist Forest; 25 September–16 October 2003.
Santa Maria Valley, Henri Pittier National Park, Venezuela; 10°22′N, 67°49′W; 530–840 m asl; Premontane Humid Forest (Ewel and Madriz, 1968); 1 August–2 September 2003.
San Gerardo Station, Children’s Eternal Rainforest, Monteverde, Costa Rica; 10°22′N, 84°47′W; 1,180–1,280 m asl; PreMontane Rain Forest; 11 January–24 February 2005.
Bajo del Tigre unit, Children’s Eternal Rainforest and adjacent private property, Monteverde, Costa Rica; 10°18′W, 84°49′N; 1,090–1,410 m asl; PreMontane Wet Forest; 10 January 2005–15 September 2006.
Middle Monteverde, private forest contiguous with reserves, Costa Rica; 10°18′W, 84°48′N; 1,465–1,600 m asl; Lower Montane Wet Forest; 22 January 2005–16 September 2006.
Montverde Cloud Forest Reserve, Costa Rica; 10°18′W, 84°48′N; 1,650–1,750 m asl; Lower Montane Rain Forest; 16 January–1 March 2005.

Statistical analyses

We used raids encountered/kilometer for each walk as our estimate of above-ground army ant foraging activity (O'Donnell and Kumar, 2006; Kumar and O'Donnell, 2009; O'Donnell et al., 2007). We tested for differences in raid encounter rates among sites using general linear models (GLM) implemented in SAS version 9.2 software. For post-hoc comparisons of means, we used Tukey's Honestly Significant Difference (HSD) test, with critical alpha set at 0.05. We performed the analyses for each army ant species alone, and for combined encounters of the two species.

Results

We encountered *L. praedator* and/or *E. burchellii* raids at all sites except the highest elevation we sampled, Lower Montane Rain Forest at Monteverde Cloud Forest Reserve (Fig. 1).We encountered a total of 83 *E. burchellii* raids

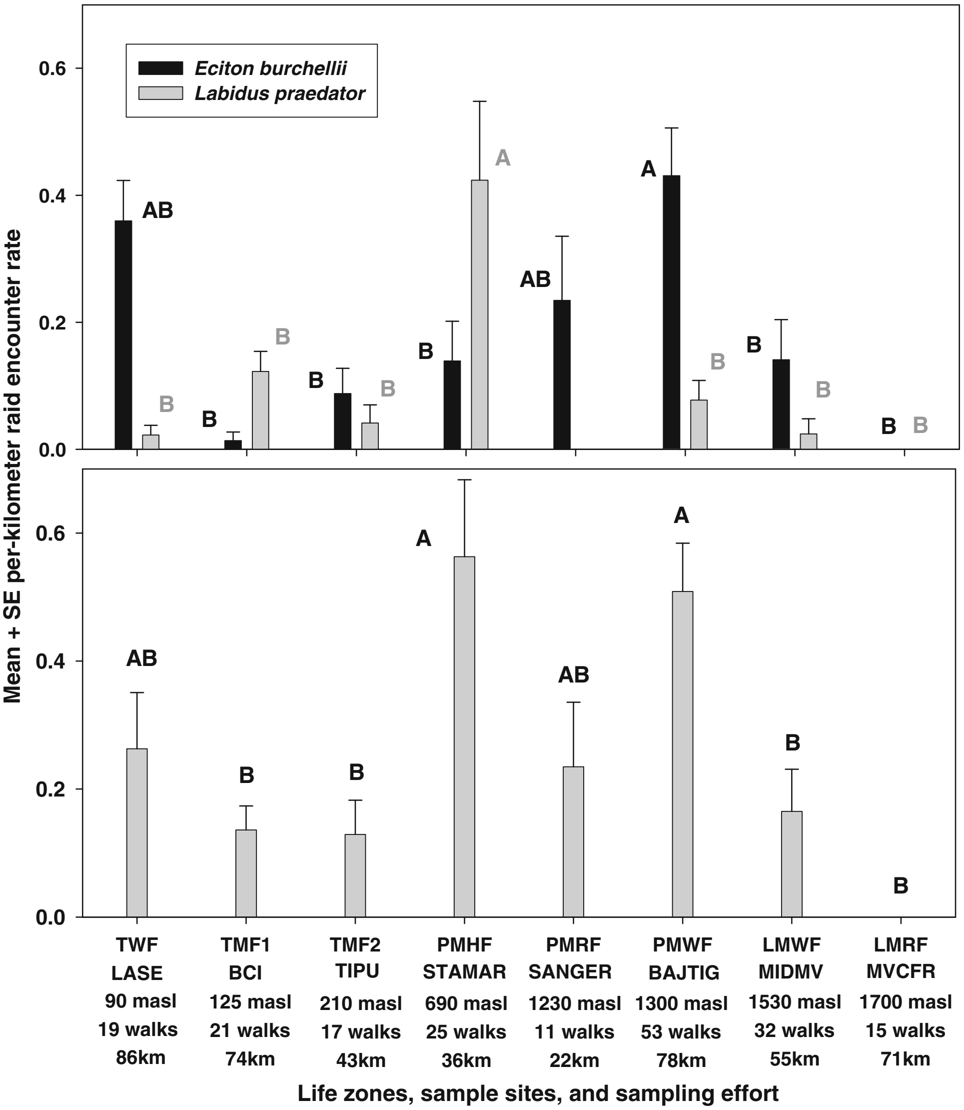

Fig. 1 Encounter rates of foraging raids of *Eciton burchellii* and *Labidus praedator* army ants during trail walk searches at eight Neotropical forest sites. The Holdridge life zone is indicated for each site. *TWF LASE* Tropical Wet Forest, La Selva; *TMF BCI* and *TIPU* Tropical moist forest, Barro Colorado Island and Tiputini; *PMHF STAMAR* PreMontane Humid Forest, Santa Maria; *PMRF SANGER* PreMontane Rain Forest, San Gerardo; *PMWF BAJTIG* PreMontane Wet Forest, Bajo del Tigre; *LMWF MIDMV* Lower Montane Wet Forest, Middle Monteverde; *LMRF MVCFR* Lower Montane Rain Forest, Monteverde Cloud Forest Reserve). The sites are arranged along the X-axis in increasing order of the midpoint elevation (m asl) of the trail walks at that site. The top graph shows per-kilometer encounter rates for the two subject species separately. The bottom graph shows total raid encounters of both species. *Letters* above the bars indicate significant pairwise differences in means among sites (Tukey's HSD test). For each site, the bottom X-axis label gives midpoint elevation (m asl), number of trail walks, and total distance walked searching for army ant raids

(0.20 raids/km overall) and 34 *L. praedator* raids (0.08 raids/km overall). The two army ant species differed significantly in their overall per-kilometer encounter rates ($F_{1,370} = 13.1$, $P = 0.0003$). The army ant species also differed significantly in their relative abundances among sites (species × site interaction term: $F_{7,370} = 5.0$, $P < 0.0001$). *Eciton burchellii* raids were more abundant than *L. praedator* raids at all sites where ants were found except Barro Colorado Island and Santa Maria (Fig. 1).

When encounters with the two species are pooled to estimate total occurrence of surface swarm-raiding army ants, the sites differed significantly in per-kilometer raid encounters ($F_{7,192} = 5.8$, $P < 0.0001$). Post-hoc analysis suggested that army ant densities were higher at two mid-elevation sites [Santa Maria (mainly due to high densities of *L. praedator*) and Bajo del Tigre (mainly due to high densities of *E. burchellii*)] than several other sites at higher and lower elevations (Fig. 1).

For *E. burchellii* alone, sites differed significantly in encounter rates ($F_{7,185} = 5.3$, $P < 0.0001$). Post-hoc pairwise comparisons showed that *E. burchellii* densities peaked in PreMontane Wet Forest at Bajo del Tigre, and were significantly higher than all other sites except La Selva and San Gerardo. For *L. praedator* alone, sites differed significantly in encounter rates ($F_{7,185} = 6.6$, $P < 0.0001$). Post-hoc pairwise comparisons showed that *L. praedator* densities peaked in PreMontane Humid Forest at Santa Maria and were significantly higher there than at all other sites.

Most of our data were collected during local wet seasons, but we collected data in both wet and dry seasons at two montane sites (Bajo del Tigre and Middle Monteverde). At these sites, overall raid encounter rates showed a non-significant trend toward being higher in the wet season (ANOVA, $F_{1,81} = 3.54$, $P = 0.064$).

Discussion

Elevational distributions of swarm-raiding army ants

The often-asserted relative rarity of swarm-raiding army ants in middle-elevation montane forests (Willis, 1966; Hilty, 1974; Willis and Oniki, 1978; Dobbs and Martin, 1998; Rios et al., 2008) was not supported by our data. Our data suggest that foraging swarm densities of both species of surface swarm-raiding army ants peak at middle elevations. Furthermore, *Labidus praedator* does not appear to range to higher elevations than *E. burchellii*.

The upper elevational limits of army ant ranges may be affected by decreases in prey density: leaf litter invertebrates, particularly ants, decreased dramatically in density going from 1,250 to 1,500 m asl along an elevational transect in Panama (Olson, 1994). However, our data suggest that surface swarm raiders reach peak densities in this elevational range, at least in Costa Rica. Abiotic constraints on the army ants themselves, including low temperatures, may be important in determining the upper elevational limits of army ant species. Species that raid above ground may be especially sensitive to thermal limitation (Kumar and O'Donnell, 2009). Above-ground army ant foraging activity and bivouac thermoregulation may be negatively affected by low ambient temperatures at elevations above 1,600 m asl in Costa Rica (Kumar and O'Donnell, 2009; T.W. Soare and S. O'Donnell, unpubl. data). Some subterranean army ant species appear to be buffered from these effects and range to much higher elevations than *E. burchellii* and *L. praedator* (Kumar and O'Donnell, 2009; J. T. Longino, pers. comm.).

The trail walk method accurately predicted *E. burchellii* colony density in lowland wet forest (Vidal-Riggs and Chaves-Campos, 2008). However, elevational variation in raid encounters during trail walks may reflect a combination of differences in colony density, as well as differences in army ant behavior, among sites. Foraging and raiding behavior differences among sites could have affected our ability to detect raids at different elevations. For example, if raids in montane forests traveled farther from the bivouac, turned less often, or lasted longer, then the higher raid encounter rates may not reflect higher colony densities. We have not quantified these elements of army ant raid behavior across sites, but the raid columns we have tracked in Monteverde appeared similar in length, directness, and diel timing to those in lowland forests. The ecological effects of swarm raids could also vary with elevation. For example, if army ant colonies and/or foraging swarms are smaller at higher elevations, their impact on prey communities could be reduced.

Implications for raid-attending birds

Our data suggest that high densities of army ant raids are available for exploitation by raid-attending birds in montane forests, particularly at middle elevations. Raid densities may not fully reflect the local value of army ant swarms as a food-generating force. If raids at higher elevations drive fewer prey items before them, either because of differences in army ant behavior or because of differences in the density, body size, or mobility of arthropod prey, then the raids' value to attending birds could be lower in montane forests. However, a diverse guild of birds attends raids in Central American montane forests (Roberts et al., 2000; Vallely, 2001; Kumar and O'Donnell, 2007). Some resident birds in Monteverde perform specialized behaviors, such as bivouac checking, that may enhance exploitation of ant swarms (Swartz, 2001; O'Donnell et al., 2010). Both the numbers and total weights of birds at raids in continuous forest in Monteverde were similar to raid-attending flock sizes in lowland forest (La Selva) (Wrege et al., 2005; Kumar and O'Donnell, 2007), and spectacularly large flocks of birds have been observed attending army ant raids in Costa Rican montane forest (Chaves-Campos, 2005).

The highest rates of encounters with raiding army ant colonies, particularly *E. burchellii*, occurred at elevations where Thamnophilidae and other obligate raid-attending birds are rare or absent (Kumar and O'Donnell, 2007; O'Donnell et al., 2010). Obligate army ant attending birds cannot persist outside the latitudinal and elevational ranges of swarm-raiding army ants. Both army ants and specialized army-ant-following birds are among the most sensitive species to forest fragmentation of lowland tropical forests, and specialized army-ant-following birds disappear from forest fragments along with army ants over time scales of weeks or even days (Willis, 1974; Bierregaard and Lovejoy, 1989; Harper, 1989; Turner, 1996). This does not necessarily imply that army ant density is the only factor that determines geographic ranges of these birds.

Our data emphasize that the ranges of obligate antbirds are not wholly congruent with the ranges of swarm-raiding army ants, particularly along elevational gradients. In both Central and South America, obligate army-ant-following antbirds drop out at about 1,000 m asl (S. O'D. pers. obs.; Willis, 1967; Hilty, 1974; Blake and Loiselle, 2000). On the Pacific slope of the Tilaran Mountain range in Costa Rica, *E. burchellii* occurs but obligate antbirds are absent from the drier; more seasonal forests that extend to sea level (S.O'D. and A. K. pers. obs.; Stiles and Skutch, 1989; Garrigues and Dean, 2007). Furthermore, the ranges of both *E. burchellii* and *L. praedator* extend north into Mexico, well above the northern limits of obligate thamnophilid antbirds (Watkins, 1976; Howell and Webb, 1995; Brumfield et al., 2007). Seasonality may be an important factor limiting the antbirds' ranges. If army ant raiding behavior changes seasonally, then swarm availability or value to specialized birds may fluctuate such that obligate or regular ant-following behavior cannot be sustained. Willis (1966) noted that there are more *L. praedator* surface swarms in wet season in Panama. Our ability to measure seasonal effects was limited, but we found some evidence that army ant raid abundance may differ between wet and dry seasons within sites.

Another possibility is that recent elevational shifts in army ant ranges occurred, possibly in response to directional climate change. If army ant elevational range limits change more rapidly than those of birds, there could be a time lag resulting in army ants at higher elevations than raid-attending birds. We have no long-term data on army ant densities in the Monteverde area. However, many local Monteverde bird species have recently shifted their elevational ranges upslope and the timing of these bird range shifts corresponded to local directional climate change (Pounds et al., 1999). These rapid bird range changes argue against short-term army ant range changes driving the patterns we documented.

The geographic and elevational range of a taxon can reflect phylogenetic history and dispersal constraints, as well as current ecological factors (Patterson et al., 1998; Blake and Loiselle, 2000). We do not know what historical and/or ecological factors, aside from army ant availability, might limit the ranges of obligate antbirds. However, the absence of obligate antbirds from montane forests may be important to local opportunities for army-ant-following by other species of birds. Obligate thamnophilid antbirds are highly aggressive at army ant swarm raids (Willis, 1966; Willis and Oniki, 1978). Direct interference competition among birds, as well as exploitation competition, plays central roles in structuring bird flocks at army ant raids and in affecting species composition of raid-attending bird communities (Brumfield et al., 2007). Montane forest army ant swarm raids in the absence of obligate antbirds may represent an especially valuable foraging resource to other bird species. Recent behavioral data suggest that a wide range of resident and migrant birds in montane forests specialize on army ant raid-attending. Some species of residents and migrants attend raids at rates higher than expected based on their local abundances, and several residents perform specialized behavior [army ant bivouac checking (Swartz, 2001)] that is associated with enhanced raid-attending (O'Donnell et al., 2010). We suggest that the relatively high density of diurnal army ant swarm raids in mid-elevation montane forests provides a predictable high-value resource to insectivorous birds.

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