Fragmentation and elevation effects on bird–army ant interactions in neotropical montane forest of Costa Rica

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Abstract: Army ants (Formicidae: Ecitoninae) are top predators in neotropical forests. Army ant raids support a community of diverse organisms, including birds that attend the raids to collect prey. While elevation and forest fragmentation influence army ant and insectivorous bird communities, their effects on the interaction between army ants and bird species is unknown. We studied the size and species composition of bird flocks attending army ant swarms in forest fragments and continuous forest across an elevational gradient (1100–1680 m asl) in a neotropical montane region (Monteverde, Costa Rica). We observed a total of 41 bird species attending army ant swarms. Neither the number of birds, nor the total body mass of birds, nor the number of bird species in attending bird flocks was related to elevation. However, we found a higher bird species richness, larger flock size and greater total body mass of birds attending army ant swarms in continuous forest. Continuous and fragmented forest shared many attending bird species in common, but there was elevational segregation of attending bird species. Some montane endemic birds, and neotropical migrants, attend swarms regularly and use army ant raids as a food source.

Key Words: antbird, cloud forest, *Eciton burchellii*, habitat alteration, *Labidus praedator*, Monteverde

INTRODUCTION

Army ants (Formicidae: Ecitoninae) are top predators in neotropical forests (Brady 2003, Franks 1982, Franks & Bossert 1983). Recent work suggests that army ants occur at much higher densities than previously recognized, and some species of army ant function as ecological keystones in neotropical forests (Boswell *et al.* 1998, Gotwald 1995, Kaspari & O'Donnell 2003). Swarms of surface-raiding species, such as *Eciton burchellii* Westwood, 1842, and *Labidus praedator* F. Smith, 1858, host a suite of diverse symbiotic organisms, including mites, beetles and centipedes (Gotwald 1995, Rettenmeyer *et al.* 1983), and swarm raids are often attended by a diverse array of bird species.

In order to escape predation by army ants, arthropods flee from the approaching raid. Some of the fleeing arthropods are preyed upon by birds that forage near army ant swarm raids (Coates-Estrada & Estrada 1989, Otis *et al.* 1986, Swartz 2001, Willis & Oniki 1978). Army ant colonies raid almost daily throughout their nomadic colony cycle (Berghoff *et al.* 2002, Boswell *et al.* 1998, Schneirla 1934, Topoff & Mirenda 1980). *Eciton burchellii*

raids also show regularity in their spacing among days (Boswell *et al.* 1998, Franks & Fletcher 1983, Gotwald 1995, Schneirla 1934, 1971). Due to the predictable and conspicuous swarming behaviour of *E. burchellii*, some neotropical lowland bird species (especially in the families Thamnophilidae and Dendrocolaptidae) regularly attend swarms in search of prey, and show behavioural adaptations to foraging at army ant raids (Roberts *et al.* 2000a, Swartz 2001, Willis & Oniki 1978, Willson 2004).

It has been suggested that the abundance of army ant colonies diminishes with increasing elevation, contributing to the absence of obligate army ant-following bird species in montane forests (Blake & Loiselle 2000, Chaves-Campos 2003, Terborgh 1977, Willis & Oniki 1978). Recent quantitative studies confirm that the density of army ant raids covaries with local net primary productivity, which generally declines with elevation, and that army ant density declines with elevation at a neotropical montane forest site (Kaspari & O'Donnell 2003, O'Donnell & Kumar 2006).

In lowland forests, habitat fragmentation affects both insectivorous birds and army ants independently (Bierregaard *et al.* 1992, Boswell *et al.* 1998, Franks & Fletcher 1983, Lovejoy *et al.* 1984, Partridge *et al.* 1996, Roberts *et al.* 2000b, Sekercioglu *et al.* 2002).

Insectivorous bird species are first to disappear from forests fragments, implying that they are particularly sensitive to habitat change (Bierregaard *et al.* 1992, Karr 1982, Sekercioglu *et al.* 2002, Willis 1974). Similarly, *Eciton burchellii* colonies disappear from forest fragments that are below a minimum size (Bierregaard *et al.* 1992, Britton *et al.* 1996, 1999, Meisel 2004, Partridge *et al.* 1996). However, the effects of fragmentation on the army ant-attending bird interaction are unknown. Furthermore, few systematic studies on army ant-bird interactions have been conducted in neotropical montane forest (Roberts *et al.* 2000a). The goal of this study was to estimate the combined effects of elevation and forest fragmentation on interactions between army ants and bird species in neotropical montane forest by quantifying bird species richness and abundance at army ant swarms.

Recent research shows that the birds attending swarms are cleptoparasites, reducing prey capture by the army ants (Wrege *et al.* 2005). Because birds rely on ant swarms for food to varying degrees, and bird attendance decreases the foraging success of the ant raids (Wrege *et al.* 2005), fragmentation and elevation effects on the interaction could have implications for both the attending birds and the ants. We tested for elevation and fragmentation effects on the potential cleptoparasitic pressure exerted by montane forest birds.

We hypothesized that army ant-bird interactions would be affected by both elevation and forest fragmentation. We made the following predictions: (1) the size and species richness of bird flocks attending army ant raids will decrease with elevation; (2) the size and species richness of bird flocks attending army ant raids will vary with habitat type, with smaller species-poor flocks in fragments relative to continuous forest; (3) the potential for cleptoparasitism of army ants by attending birds will be affected by habitat fragmentation; and (4) bird species will vary in their rate of attendance at army ant raids. We were particularly interested in assessing whether some montane forest resident birds, and neotropical migrants, attend swarms regularly. Those that do may rely on army ant raids as a food source.

METHODS

Study area

The research was conducted in neotropical montane forest in the Monteverde area, Costa Rica (10°18′N, 84°47′W). Monteverde is a well-studied cloud-forest habitat on the continental divide of the Tilarán mountain range. Local habitats include privately protected continuous forest and adjacent forest fragments (Guindon 1997, Haber 2000, Harvey 2000). Over small changes in elevation, the habitat changes dramatically.

Five Holdridge life zones occur within a 600-m elevation range at Monteverde (Haber 2000, Holdridge 1966). The present study was conducted in continuous forest (11 sites) and forest fragments (7 sites) located between 1100 m asl and 1680 m asl on the Pacific and Atlantic slopes in the vicinity of Monteverde.

Opportunistic observations of birds at army ant swarms

In the dry season of 2005 (12 January to 4 March) we collected data on army ant density and diversity in the Monteverde area (O'Donnell & Kumar 2006). Army ant raids were sampled using standardized trail walks at four elevationally separated sites, ranging from 1200 to 1650 m asl, and army ant activity was observed opportunistically at other locations in the Monteverde area. When a swarm raid front was encountered, we noted whether birds were in attendance. Birds were identified to species and we counted individuals when possible. To be counted, birds had to be actively foraging either within 2 m of the front of the swarm, or in the army ant swarm. All dry-season data were collected in continuous forest.

Standardized observations of birds at army ant swarms

Standardized observations of bird attendance at army ant swarms (*Eciton burchellii* and *Labidus praedator*) were made from 29 June to 11 December 2005. We observed a maximum of one swarm per day and alternated sampling dates among elevations and habitat types to minimize order effects. Army ant swarms were located by walking trails, and by referral from other observers to A.K. After locating an army ant colony, the foraging trail was followed to the swarm front where the attending birds forage (Swartz 2001, Willis & Oniki 1978). The following data were collected: (1) Start and end time. (2) Habitat type (continuous or fragment). Habitat type was determined by viewing aerial maps, by consulting Guindon (1997), and during site visits. A fragment was defined as any patch of forest separated from another patch by at least 50 m of open habitat. We used fragments ranging in size from approximately 1 ha to 4 ha (Guindon 1997). (3) Elevation (all elevations were taken to the nearest 1 m with a digital altimeter).

The best spot for viewing the swarm front was chosen; this was usually located off to one side and facing in the direction in which the swarm was moving. The observation period began 5 min after reaching the swarm front to allow the birds to resume their normal activities (Coates-Estrada & Estrada 1989). Each observation period lasted 60 min total, unless the ants traversed over unmanageable terrain or heavy rain began. We recorded bird attendance at the army ant swarm. To be counted

as an attendant, a bird had to be seen collecting prey that was fleeing from the ants, or approaching within 5 m of the swarm front from above (for woodcreepers (Dendrocolaptidae) and other birds that normally forage from tree trunks). For each attending flock we recorded: (1) bird species (nomenclature follows Stiles & Skutch 1989); and (2) number of individuals of each bird species present. Each time the flock composition at the swarm front changed, time (to the nearest second), bird species, and number of individuals per species was recorded again. A bird was counted as leaving the flock if it flew out of sight more than 5 m away, as opposed to being temporarily obscured by vegetation. Observation bouts when no birds were present were also noted.

Data analyses

We assumed that different sites housed different army ant colonies. Because we did not track ant colonies, some of the observations at a site could have been made on swarms from the same army ant colony. Therefore, we included site as a cofactor in the statistical analyses.

Since the birds were not banded, we could not distinguish individuals that left and returned from newly arriving swarm attendants. As a conservative estimate of individual abundance per bird species per observation bout, we used the largest number of individuals that were observed simultaneously at the swarm. The number of birds and bird species attending army ant swarms were analysed for elevation and habitat effects using analysis of covariance (ANCOVA) implemented in SAS 9.1 (SAS Institute Inc., Cary, NC). All data met the assumptions of parametric analysis (Levene's test for equality of error variances and tests for normality; Pedhauzer 1982).

To assess total attending bird species richness in continuous and fragmented habitats, we used EstimateS Version 7.5 software (http://purl.oclc.org/estimates). We computed both observed (MaoTau) and estimated (Abundance Coverage Estimator-ACE) bird species richness. Species accumulation curves were based on individual abundances of birds in each habitat type, and in total. Individual abundances were conservatively estimated, as described above.

We analysed the amount of overlap in attending bird species (beta diversity) between habitat types, and across elevations, in two ways. First, we calculated the Chao-Jaccard abundance-based diversity statistic. This statistic estimates the probability that a bird randomly drawn from each of two samples will belong to a species that is shared between the samples (Chao *et al.* 2005, EstimateS, Version 7.5). Second, we calculated observed numbers of species shared and an extrapolated estimate of the number of species shared using the Chao Shared Estimate statistic (EstimateS, Version 7.5). We used the same methods to estimate bird species shared between continuous-forest and forest-fragment samples, pooled across all elevations.

To test for elevational segregation in attending bird species, we divided the data into three elevation blocks, such that the blocks were as similar as possible in sample size (number of army ant swarms). Each army ant swarm watched was counted as a sample. Each elevation block was pooled across continuous and fragmented forest. We did not include data from two Atlantic-slope sites, or from one low-elevation Pacific-slope site, because too few samples were taken at these elevations.

To analyse the potential cleptoparasitic pressure the birds exerted on swarms, we calculated the per-minute average number of birds present during each observation session. Because the total body mass of attending birds also affects the ants' foraging success (Wrege *et al.* 2005), we also estimated the per-minute average mass of the attending birds. Bird body mass values were species averages taken from Stiles & Skutch (1989). We tested for habitat (continuous forest versus fragment) effects on the size and mass of attending flocks using ANOVA implemented in SAS 9.1 (SAS Institute Inc. 2002–2004).

RESULTS

Opportunistic observations: the montane ant-following bird community

Birds were seen at surface swarm raids of three army ant species: *E. burchellii*, *L. praedator* and *Labidus spininodis* Emery, 1890. We encountered 27 swarms of these species, of which 17 (63%) were attended by birds. Twenty bird species were recorded during opportunistic observations. We observed three bird species during the dry season that we did not observe during the wet-season standardized observations (Table 1).

Standardized observations: the montane ant-following bird community

We sampled at 32 swarms in continuous forest habitat (*E. burchellii*: n = 29; *L. praedator*: n = 3) and 26 swarms in forest fragments (*E. burchellii*: n = 26). Analyses on *E. burchellii* swarms alone did not change the conclusions, so the *L. praedator* observations were included in the analyses. Overall we observed 38 bird species from 16 families attending army ant raids in the Monteverde area, including seven species of latitudinal migrants (Table 1). Two species of latitudinal migrants were seen only in fragments. Birds ranged in size from 7 g to 295 g body mass. Although most of the attending birds were insectivores, several feeding guilds were represented including

Table 1. Species list and occurrence of birds attending army ant swarms in montane forest, Monteverde, Costa Rica. Bold entries are species that were not observed at Monteverde army ant swarms by Vallely (2001). An asterisk indicates Nearctic migrants. Sample sizes were, Continuous forest: 32 swarms; Forest fragments: 26 swarms; Opportunistic samples: 27 swarms. Bird species names from Stiles & Skutch (1989). Abbreviations: contin. = continuous, num. = number, quant. = quantitative and opportun. = opportunistic.

Attending bird species	Per cent (num.) contin. forest present	Per cent (num.) fragment present	Total % in quant. samples	Per cent (num.) in opportun. samples
Orange-billed nightingale thrush (*Catharus aurantiirostris*) Turdidae	44.0(14)	50.0(13)	47	7.00(2)
White-eared ground sparrow (*Melozone leucotis*) Emberizidae	41.0(13)	39.0(10)	40	11.0(3)
Blue-crowned motmot (*Motmotus momota*) Momotidae	34.0(11)	8.00(2)	22	7.00(2)
Rufous-and-white wren (*Thryothorus rufalbus*) Troglodytidae	25.0(8)	12.0(3)	19	–
Brown jay (*Cyanocorax morio*) Corvidae	15.6(5)	19.2(5)	17	–
*Kentucky warbler (*Oporornis formosus*) Parulidae	–	30.8(8)	14	–
Ruddy woodcreeper (*Dendrocincla homochroa*) Dendrocolaptidae	18.8(6)	3.84(1)	12	7.00(2)
Plain wren (*Thryothorus modestus*) Troglodytidae	12.5(4)	7.69(2)	10	–
Slaty-backed nightingale thrush (*Catharus fuscater*) Turdidae	19.0(6)	–	10	19.0(5)
Clay-coloured thrush (*Turdus grayi*) Turdidae	9.38(3)	7.69(2)	9	7.00(2)
Emerald toucanet (*Aulacorhynchus prasinus*) Ramphastidae	15.6(5)	–	9	–
Yellowish flycatcher (*Empidonax flavescens*) Tyranidae	9.38(3)	3.84(1)	7	11.0(3)
White-throated thrush (*Turdus assimilis*) Turdidae	12.5(4)	–	7	4.00(1)
Immaculate antbird (*Myrmeciza immaculate*) Thamnophilidae	13.0(4)	–	7	29.0(8)
Rufous-capped warbler (*Basileuterus rufifrons*) Parulidae	12.5(4)	–	7	4.00(1)
*Wood thrush (*Hylocichla musterlina*) Turdidae	6.25(2)	3.84(1)	5	4.00(1)
Barred woodcreeper (*Dendrocolaptes certhia*) Dendrocolaptidae	6.25(2)	3.84(1)	5	–
White-throated spadebill (*Platyrinchus mystaceus*) Tyrannidae	3.13(1)	7.69(2)	5	–
Slate-throated redstart (*Myioborus miniatus*) Parulidae	9.38(3)	–	5	7.00(2)
Ruddy-capped nightingale thrush (*Catharus frantzii*) Turdidae	9.38(3)	–	5	4.00(1)
Grey-breasted wood wren (*Henicorhina leucophrys*) Troglodytidae	3.13(1)	3.84(1)	3	4.00(1)
Black-headed nightingale thrush (*Catharus mexicanus*) Turdidae	3.13(1)	3.84 (1)	3	–
Chestnut-capped brush-finch (*Atlapetes brunneinucha*) Emberizidae	3.13(1)	3.84(1)	3	–
Three-striped warbler (*Basileuterus tristriatus*) Parulidae	6.25(2)	–	3	4.00(1)
Squirrel cuckoo (*Piaya cayana*) Cuculidae	6.25(2)	–	3	–
*Wilson's warbler (*Wilsonia pusilla*) Parulidae	6.25(2)	–	3	–
Common bush-tanager (*Chlorospingus ophthalmicus*) Thraupidae	3.13(1)	–	2	4.00(1)
Tufted flycatcher (*Mitrephanes phaeocercus*) Tyranidae	3.13(1)	–	2	4.00(1)
Yellow-throated brush finch (*Atlapetes gutturalis*) Emberizidae	3.13(1)	–	2	–
Barred forest falcon (*Micrastur ruficollis*) Falconidae	3.13(1)	–	2	–
Black-and-white warbler (*Mniotilta varia*) Parulidae	3.13(1)	–	2	–
Black-billed nightingale thrush (*Catharus gracilirostris*) Turdidae	3.13(1)	–	2	–
***Black-throated green warbler (*Dendroica virens*) Parulidae**	3.13(1)	–	2	–
Black-throated wren (*Thryothorus atrogularis*) Troglodytidae	3.13(1)	–	2	–
***Canada warbler (*Wilsonia canadensis*) Parulidae**	3.13(1)	–	2	–
Chiriqui quail dove (*Geotrygon chiriquensis*) Columbidae	3.13(1)	–	2	–
Golden-crowned warbler (*Basileuterus culicivorus*) Parulidae	3.13(1)	–	2	–
White-breasted wood wren (*Henicorhina leucosticta*) Troglodytidae	3.13(1)	–	2	–
Yellow-faced grassquit (*Tiaris olivacea*) Emberizidae	3.13(1)	–	2	–
Spot-crowned woodcreeper (*Lepidocolaptes affinis*) Dendrocolaptidae	–	3.84(1)	2	–
*Swainson's thrush (*Catharus ustulatus*) Turdidae	–	3.84(1)	2	–
Azure-hooded jay (*Cyanolyca cucullata*) Corvidae	–	–	0	7.00(2)
Olivaceous woodcreeper (*Sittasomus grisecapillus*) Dendrocolaptidae	–	–	0	4.00(1)
Rufous-breasted antthrush (*Formicarius rufipectus*) Formicariidae	–	–	0	4.00(1)

frugivores, granivores, and a raptor. Most attending bird individuals and species were not from families that include co-adapted, high-fidelity army ant followers.

## Elevational and fragmentation effects on bird attendance at army ant swarms

The number of bird species at swarms was not affected by elevation (Figure 1a: ANCOVA $F_{1,54} = 0.06$, P = 0.81). However, bird flock species richness differed significantly between the habitat categories. More bird species were present at swarms in continuous forest (mean ± SE = 3.9 ± 0.53 bird species per swarm; range = 0–10 spp.) than in fragments (2.4 ± 0.47 bird species per swarm; range = 0–7 spp.) (Figure 1a: ANCOVA $F_{1,54} = 4.81$, P = 0.033). The habitat effect on the number of bird species per swarm did not differ across elevations (Figure 1a: ANCOVA test for heterogeneity of slopes $F_{1,54} = 0.84$, P = 0.36).
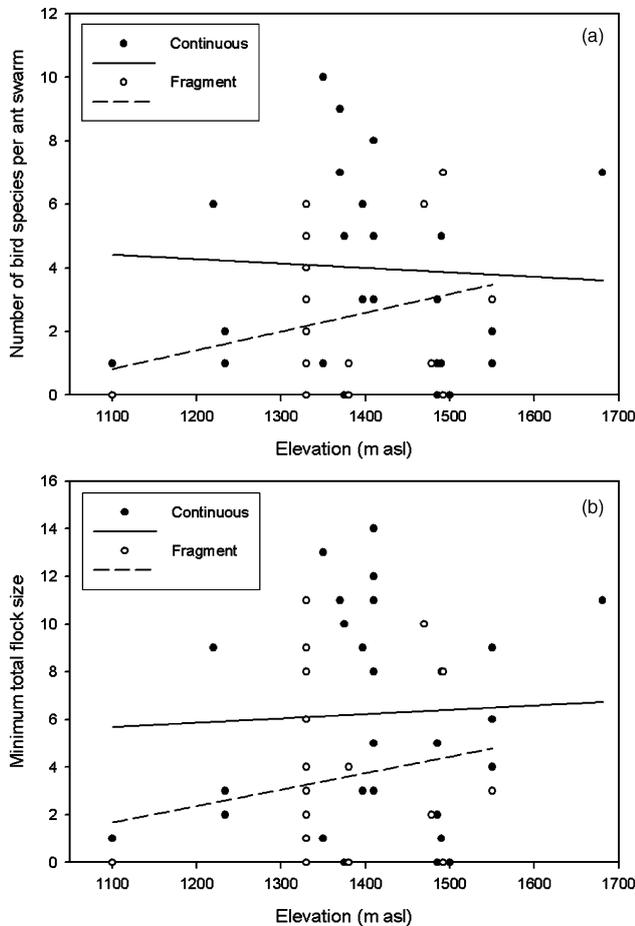
Figure 1. The relationships of attending flock composition with elevation and habitat type. The number of bird species observed at army ant swarms plotted against elevation, separated by habitat type (a). The flock size of birds attending army ant swarms plotted against elevation, separated by habitat type (b). Flock size was determined by the minimum number of birds present at swarms summed across species. Swarms observed in different habitat types (continuous and fragmented forest) are indicated by shading. Lines represent linear regression best fit of the number of species (a) or flock size (b) against elevation, within each habitat type. For forest fragments: Number of birds $= -5.9 + (0.007)$ (elevation), $R^2 = 0.03$, $P = 0.31$; Number of bird species $= -5.7 + (0.006)$ (elevation), $R^2 = 0.04$, $P = 0.43$. For continuous forest: Number of birds $= 3.7 + (0.002)$ (elevation), $R^2 = 0.002$, $P = 0.78$; Number of bird species $= 5.9 + (-0.001)$ (elevation), $R^2 = 0.003$, $P = 0.81$.

The number of birds attending swarms was not affected by elevation (Figure 1b: ANCOVA $F_{1,54} = 0.36$, $P = 0.55$). Summing across bird species, flocks of attending birds were larger at swarms in continuous forest (6.1 ± 0.83 birds present; range $= 0$–14 birds) than in fragments (3.5 ± 0.65 birds present; range $= 0$–11 birds) (Figure 1b: ANCOVA $F_{1,54} = 6.04$, $P = 0.017$). The habitat effect on flock size did not differ across elevations (Figure 1b: ANCOVA test for heterogeneity of slopes $F_{1,54} = 0.18$, $P = 0.68$).
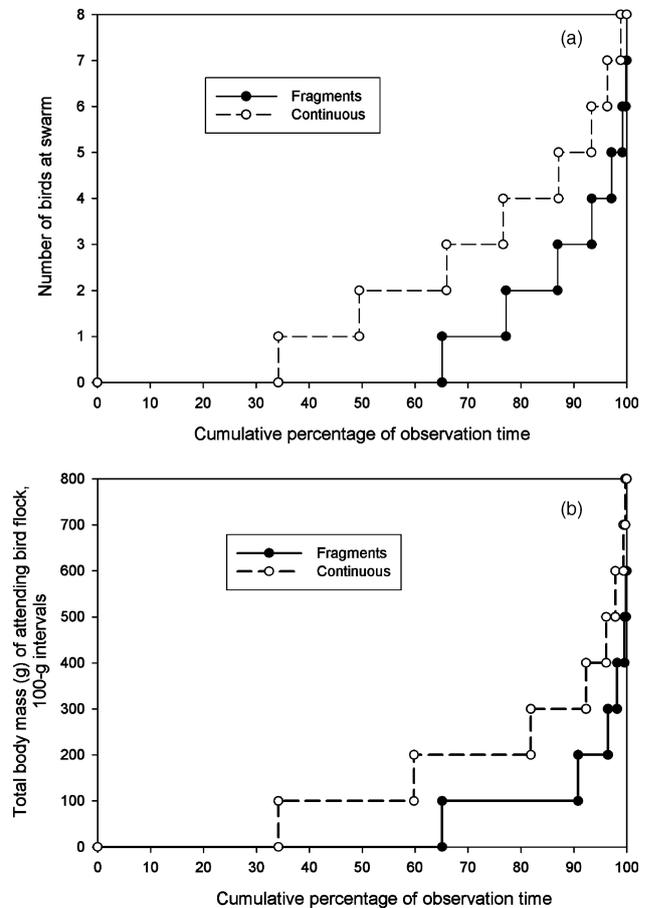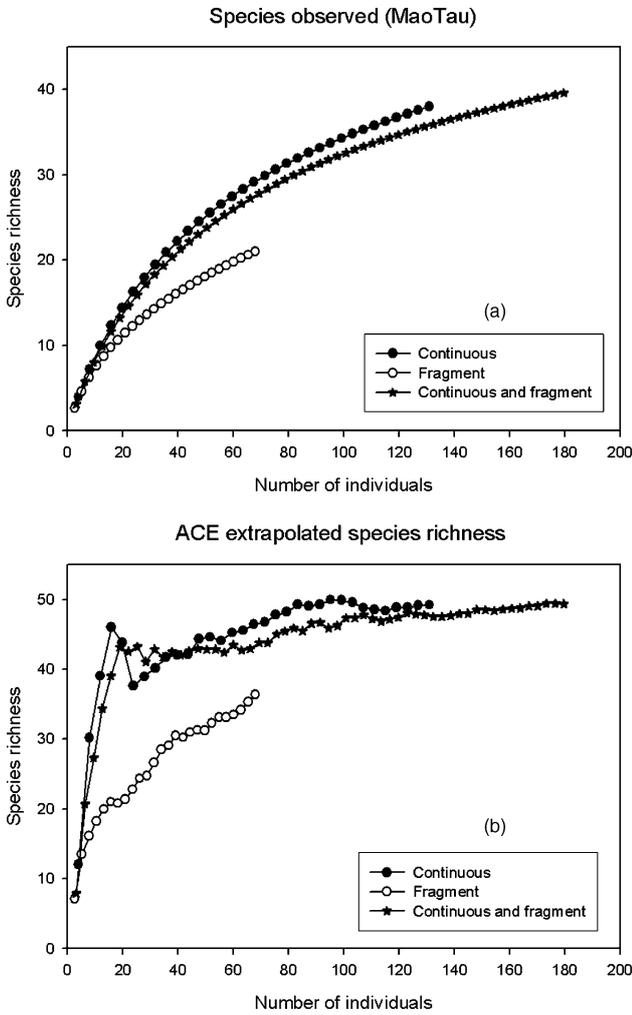

Figure 2. Estimate of the cleptoparasitic pressure of birds on army ants in forest fragments and continuous forest, plotted as the cumulative percentage of time different flock sizes were present at army ant swarms (a), and the total mass of birds present at army ant swarms (b).

Bird pressure on army ant swarms

To better estimate the potential cleptoparasitic pressure the bird flocks might exert on army ant swarms, we calculated the amount of time that swarms in continuous forest and fragments were attended by bird flocks of different sizes and mass. Both the mean numbers and total body masses of birds in attendance (average per minute) were higher for swarms in continuous forest (Figure 2a: for number of birds: $F_{1,56} = 11.4$, $P = 0.0013$, Figure 2b: for mass of birds: $F_{1,56} = 5.26$, $P = 0.026$).

Patterns of bird species richness

In continuous forests we observed 37 bird species, while in fragments we observed 19 bird species. Species accumulation curves confirm that the total bird species richness was higher in continuous habitats than in fragments (Figure 3a). We did not observe an asymptote on the species accumulation curves, suggesting that

Species observed (MaoTau)

(a)

		Continuous
		Fragment
		Continuous and fragment

ACE extrapolated species richness

(b)

		Continuous
		Fragment
		Continuous and fragment

Figure 3. Species accumulation curves representing abundance-based data for bird species attending army ant swarms in two habitat types (fragmented and continuous forest) and in total, in the Monteverde area for observed species richness (Mao Tau) (a) and extrapolated species richness (Abundance Based Coverage Estimator) (b). Individuals are total number of birds attending army ant swarms.

observations at more swarms would have yielded new attending bird species. The extrapolated number of potential attending bird species was higher in continuous forest (Figure 3b). The total extrapolated number for swarm-attending bird species was 55.8. However, while the con-

tinuous forest extrapolation approached an asymptote of 49.2 species, the fragment and total extrapolations were still climbing at the end of our sampling.

Elevation and fragmentation effects on species of bird attending swarms

We observed 16 shared species among continuous and fragmented habitats, and an extrapolated estimate of 27 species shared (Chao-shared estimate statistic). The estimated probability of bird co-occurrence between forest fragments and continuous forest was 0.74 (Chao-Jaccard estimated abundance-based statistic).

We calculated the amount of species sharing among three elevation blocks in the Monteverde area (Table 2). Estimated bird co-occurrence between the low- and middle-elevation blocks was highest, and species co-occurrence was lowest between the low- and high-elevation blocks. These patterns suggest elevational segregation of attending bird species.

The number of bird species differed among elevation blocks (Table 2). The largest species richness was observed in the middle block (23 species) followed by the highest block (21 species) and the lowest block (16 species). We calculated the observed and extrapolated bird species sharing among the three elevation blocks in the Monteverde area (Table 2). The highest amount of species sharing (observed and extrapolated) was between the middle and high blocks (13 species observed, 40 species extrapolated) while the lowest amount of sharing (observed and extrapolated) was between the lowest and highest elevation blocks (7 species observed, 9.5 extrapolated).

We found evidence for elevational replacement of attending bird species from two genera. Within the genus *Catharus*, *C. fuscater* (slaty-backed nightingale-thrush) and *C. aurantiirostris* (orange-billed nightingale-thrush) are elevationally segregated residents in Monteverde. From 1100 to 1470 m asl we observed 53 of 54 (98%) of *C. aurantiirostris* raid attendants, while from 1550 to 1680 m asl we observed 16 of 17 (94%) *C. fuscater* attendants. Within the genus *Basileuterus*, *B. rufifrons* (rufous-capped warbler) and *B. tristriatus* (three-striped warbler) are

Table 2. Bird species sharing among elevations. Estimated amount of species sharing for birds flocks attending army ant swarms in three elevational blocks in the Monteverde area (above diagonal). Values presented are the Chao–Jaccard-Estimated abundance-based species overlap index. Observed and extrapolated numbers of army ant-attending bird species shared among three elevational blocks in the Monteverde area (below diagonal). Observed overlap in species richness is in normal print while extrapolated overlap is in parentheses.

	1322–1350 m asl (20 swarms observed)	1370–1410 m asl (16 swarms observed)	1470–1550 m asl (16 swarms observed)
1322–1350 m asl	–	0.74	0.29
1370–1410 m asl	10 (10.4)	–	0.58
1470–1550 m asl	7 (9.5)	13 (40)	–

elevationally segregated residents in Monteverde. From 1330 to 1397 m asl we observed 9 of 9 (100%) of the *B. rufifrons* attendants, and from 1410 to 1490 m asl we observed 3 of 3 (100%) of the *B. tristriatus* attendants.

DISCUSSION

Birds attending army ant raids in montane forests

It is often assumed that fewer obligate ant-following bird species occur in neotropical montane forests because of lower densities of army ant colonies, relative to lowland forests (Blake & Loiselle 2000, Chaves-Campos 2003, Terborgh 1977, Willis & Oniki 1978). However, it may not always be the case that species richness of bird attendants is lower in montane habitats. We did not find evidence that richness of bird flocks differed with elevation over the 1100–1680 m asl range of our study. Vallely (2001) noted 50 bird species at army ant swarms in the Monteverde area, including 22 species that we did not record. We recorded 12 bird species Vallely (2001) did not record, so between our studies, a total of 62 bird species have been recorded at army ant swarms in the Monteverde area. Species accumulation curves and species richness extrapolations both suggest that our sampling of attendant bird species was not complete, and that more bird species would be observed at Monteverde swarms with additional sampling effort. At La Selva, a lowland forest on the Atlantic slope of Costa Rica, 20 bird species were observed regularly foraging with army ant swarms (Chaves-Campos 2003). In Panama, Roberts *et al.* (2000a) observed 126 bird species from 28 families attending swarms in an elevation range from 1400 m to 1800 m asl. In lowland forests, Coates-Estrada & Estrada (1989) observed 43 bird species attending both *E. burchellii* and *L. praedator* swarms in Mexico (160–550 m asl). Willis & Oniki (1978) estimate that there are 50 species of birds reliant on army ant swarms in lowland wet forests, although there are more than 200 bird species that have been noted at army ant swarms in Panama in long-term studies. The community of army ant-following bird species is diverse across a wide elevational range, and army ant swarms may be an important food resource for birds in montane habitats.

Reliance of birds on army ants

In lowland forests, attending bird species range in their degree of fidelity to follow army ant colonies, and presumably in their degree of reliance on the ant raids for food (Chaves-Campos 2003, Swartz 2001, Willis & Oniki 1978). It is likely that the variation in swarm attendance rates that we observed also reflects bird species differences in reliance on ant swarms for food.

The only Monteverde bird species listed as an army ant follower by Willis & Oniki (1978) is *Myrmeciza immaculata* (immaculate antbird). There were several species in our study that were in attendance at more than 20% of army ant raids in the quantitative samples: *Catharus aurantiirostris* (orange-billed nightingale-thrush), *Melozone leucotis* (white-eared ground sparrow), *Motmotus momota* (blue-crowned motmot). Other species were in attendance at similarly high frequencies at a subset of elevations, or only in forest fragments. It is important to note that while families that include high-fidelity, coevolved army ant-following birds were present (Dendrocolaptidae and Thamnophilidae), attendance by birds in other families was higher. Such high frequencies of attendance suggest that food taken from army ant raids represents an important component of the diet of these birds. A critical test of this assertion could include time-budget analysis and feeding-rate studies of individually marked birds.

We observed seven species of North American migrant attending army ant swarms in the Monteverde area. Latitudinal migrants attended swarm raids across all elevations in our study. At lowland sites, the numbers of irregular ant followers are similarly augmented by migrants from North America (Willis & Oniki 1978).

Elevation effects

Rate of bird attendance was not affected by elevation, but the species composition of flocks was. Although we sampled a small elevational range (580 m), previous work in the Monteverde area has shown dramatic changes in plant and animal communities across the same elevation range (Haber 2000, Pounds 2000, Young & MacDonald 2000). Bird community species composition often changes rapidly with elevation in the Neotropics (Blake & Loiselle 2000, Terborgh 1971, Young *et al.* 1998). Blake & Loiselle (2000) found that bird species composition changed substantially from 500 m to 1000 m asl in Costa Rica, and that bird species richness declined sharply above 1500 m asl. In the Monteverde area there is evidence of both high bird species turnover across elevations and declining bird species richness with elevation (Young *et al.* 1998). Many bird genera with more than one resident species exhibit a pattern of elevational replacement in Monteverde (Terborgh 1971, Young *et al.* 1998), and we found evidence of elevational replacement among army ant attendants in the genera *Catharus* and *Basileuterus*.

Fragmentation effects

We observed birds foraging at army ant swarms in both continuous forest and fragments. We found that the size and mass of attending flocks was lower in forest

fragments. Our study was not designed to determine the relative importance of these habitat categories to either the ants or the attending birds, and there are a number of non-exclusive explanations for the habitat patterns we observed.

First, lower bird attendance in fragments could be caused by lower overall bird densities and diversities in fragments. Bird species richness declines as the amount of forest area declines, a pattern noted especially in insectivorous bird species (Brown & Sullivan 2005, Stouffer 2007, Stouffer & Bierregaard 1995, Watson et al. 2004). Insectivorous bird species may be less likely to occur within forest fragments either due to a lower density of arthropod prey items or large territorial area requirements that cannot be maintained in fragmented habitats (Burke & Nol 1998, Stouffer 2007, Zanette et al. 2000). The size of the forest fragments may also affect the bird species composition within the fragments. A critical test of the effect of fragment size on bird species composition would include sampling differently sized fragments at the same elevation.

Second, while some insect species densities increase in fragments, there is evidence to suggest that wasp and ant densities, important prey to some army ants, decline in fragments (Bierregaard et al. 1992, Laurance et al. 2002). Lower prey densities may cause army ants to avoid forest fragments, disrupting the species interaction between army ants and ant-following birds.

Finally, fragmentation may be affecting the army ants directly. Eciton burchellii colonies disappear from forest fragments that are below a minimum size (Bierregaard et al. 1992, Britton et al. 1996, 1999; Meisel 2004, Partridge et al. 1996). Roberts et al. (2000b) compared the raid behaviour of the swarm-raiding army ants E. burchellii and Labidus praedator in intact neotropical pre-montane moist forest in Panama (1200–1800 m asl), shade coffee plantations and sun coffee plantations. Neither species was seen foraging in sun coffee plantations, and they foraged less often in shade coffee than continuous forest, suggesting that habitat alteration can affect army ant behaviour in montane forest.

Ant-following birds decrease the prey available to army ants at swarms, acting as cleptoparasites (Wrege et al. 2005). Both flock size and total biomass incur proportional and independent costs on the foraging success of the army ants (Wrege et al. 2005). Our findings raise the interesting possibility that army ants in forest fragments may suffer less cleptoparasitic pressure than raids in adjacent continuous forest. The net pressure from bird cleptoparasites will depend, in part, on the distribution of resources (prey) in continuous versus fragmented forest.

Habitat fragmentation can cause shifts in species composition through local extinction, and may cause additional indirect biotic effects on communities through changes in species interactions (Crooks & Soulé 1999, Jiang & Kulczycki 2004, Laurance 2005). Conversely, as area around forest reserves becomes deforested, the remaining forest fragments play an increasingly important role in maintaining faunal diversity (Ferraz et al. 2003, Guindon 1997) and related biological processes (Laurance 2005). Our data show that fragmentation affects army ant-bird interactions in montane forest, but also emphasizes that birds in fragments may still rely on army ant swarms for food. Latitudinal migrants were seen attending swarms in forest fragments at higher rates, emphasizing the potential importance of these habitats to some migrant insectivorous birds.

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