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ANTBIRD GUILDS IN THE LOWLAND CARIBBEAN RAINFOREST OF SOUTHEAST NICARAGUA[1]

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Abstract. Some 20 species of antbirds occur in lowland Caribbean rainforest in southeast Nicaragua where they form five distinct guilds on the basis of habitat preferences, foraging ecology, and foraging behavior. Three guilds are habitat-based, in Edge, Forest, and Gaps within forest; two are behaviorally distinct, with species of army ant followers and those foraging within mixed-species flocks. The guilds each contain 3–6 antbird species. Within guilds, species are segregated by body size differences between member species, and in several guilds are evenly spaced on a logarithmic scale of body mass. Among guilds, the factors by which adjacent body sizes differ vary between 1.25 and 1.75. Body size differences may be related to differences in preferred prey sizes, but are influenced also by the density of the vegetation in which each species customarily forages.

Resumen. Unas 20 especies de aves hormigueras viven en el bosque tropical perennifolio, sureste de Nicaragua, donde se forman cinquo gremios distinctos estribando en preferencias de habitat, ecologia y comportamiento de las costumbres de alimentacion. Las diferencias entre las varias especies son cuantificadas por caractaristicas del ambiente vegetal y por la ecologia y comportamiento de la alimentación, y usados para definir cinco grupos o gremios ("guilds"). Tres gremios se designan por las relaciones de habitat: edge (margen), forest (selva), y gaps (aberturas adentro la selva); dos mas por comportamiento, partidarios de army ants (hormigas armadas) y mixed-species flocks (forrejando en bandadas de especies mexcladas). Estos gremios contenien 3–6 especies hormiguera. Dentro de grupos hay diferencias regulares en peso de cuerpo entre las especies; diferencias que igualmente existen entre los gremios diferentes, con razónes medios de 1.25 a 1.75 en peso de cuerpo. Las diferencias en el tamaño de especies individuales probablemente estan relaciónadas con las diferencias entre los tamaños de las presas preferidas, pero quizas son influenciadas por la densidad de la vegetacion en donde se alimentan.

Key words: antbirds, body size, foraging behavior, foraging height, guild, size segregation.

INTRODUCTION

Antbirds currently comprise two Neotropical families (Formicariidae and Thamnophilidae; AOU 1997) of ca. 250 species. Most are generalized insectivores of forest, forest edge, or gaps within the forest; some habitually consort in multispecies flocks that forage in the forest understory or subcanopy, and a minority (10% according to Willis and Oniki, 1978) follow army ant swarms. Local assemblages of antbirds number up to several dozen species in lowland Amazonia (Rio Napo, eastern Ecuador: 31 species [Bochan, unpubl. data]; Rio Manu area, Peru: 53 species [Terborgh et al. 1984]; Belem, Brasil: 17 common species among mistnet samples [Lovejoy 1974]). In Central America, species counts are lower (La Selva, Costa Rica: 18 resident species [Stiles 1983]; Barro Colorado Island, Panama: 15 species, some now rare or extinct [Willis and Eisenmann 1979]).

Most studies of community composition, ecological segregation, or interspecific relationships in antbirds have been conducted on either ant-following or mixed-flock species. Pearson (1977) studied the ecological relationships of small antbirds typical of mixed-species subcanopy flocks in Peru, where Munn (1980) recorded some 17 antbird species in understory and canopy flocks. Jones (1977) investigated territorial and foraging attributes of the antwrens of mixed-species flocks in Panama; Gradwohl and Greenberg (1980) studied flock formation and behavioral interactions at the same site. Similar work has been conducted on antwren flocks in Ecuador (Whitney 1994). Detailed life histories have been published on several ant-following species (Willis 1967, 1968, 1973) and their behavior (Oniki 1971, 1972, Oniki and Willis

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1972, Willis and Oniki 1978). However, relatively little is known of the more usual territorial species of non-antfollowers of forest, edge, and second-growth habitats (Howell 1957, Willis 1983).

I present observations on antbirds from a lowland tropical forest site in southeastern Nicaragua. The distributions, habitat preferences, and foraging ecology of 19 of the 20 species expected at this site are reported here, with particular reference to ecological segregation by habitat, foraging behavior and height, and body size, and summarized by species allocation to five antbird guilds.

METHODS

STUDY SITE

The observations reported here were made April–May 1994 and 1999 at Refugio Bartola and the Gran Reserva Biologica "Rio Indio-Maiz" in southeastern Nicaragua. The site is located at the confluence of the Rio Bartola and the Rio San Juan, on the east and west banks of the former and the north bank of the latter (10.97°N, 84.16°W, elev. 30 m). The climate is wet tropical, with around 4 m of annual precipitation, and a dry season from February–April during which about 15% of the annual rainfall is recorded. During the study periods, 100 mm of precipitation fell in 1994, 160 mm in 1999. Temperatures were equable in this period, generally around 23°C at dawn, occasionally reaching 36°C in the open on cloudless days, and 31°C within the forest.

The vegetation in this area is lowland tropical rainforest; within the Gran Reserva, some half million hectares of pristine lowland rainforest are protected (although precariously), constituting perhaps the largest extent of primary forest in Central America. Canopy trees reach >50 m in height, and the composition of the forest appears similar to that at La Selva, Costa Rica (100 km to the southwest), although the dominant forest tree *Pentaclethra macroloba* is less common at the Bartola and *Dipteryx panamensis* more so (Hartshorn 1983).

Although most of the vegetation in the vicinity of the site is primary forest, there are natural edge habitats besides those around abandoned clearings. They include forest edges along the banks of the major rivers and within the forest along the larger streams, and around tree-fall gaps that are either natural or the result of a few, select tree removals for lumber needs. Within the study site are several areas of second growth, resulting from clearing for small *fincas* (abandoned 5–15 years ago) and around the Refugio buildings and Gran Reserva guard station.

This site supports a high diversity of the plant and animal species typical of undisturbed lowland rainforest. Over the two visits, 256 bird species were recorded in ca. 1 km^2, with a jackknife estimate (based on species seen only in one or the other visit) of 298 bird species. Among species recorded are a number which typically are lost from disturbed sites, such as many mammals (primates, felids, edentates, and tapirs), three cracids, and two species of *Ara* macaws.

PROCEDURES

Antbirds were located by sight and sound within 1.5 km of the Refugio both east and west of the Rio Bartola. Antbird songs are distinctive (Stiles and Skutch 1989), and are useful phenotypic characters in studies of antbird systematics (Isler et al. 1998, 1999) and in the recognition of new species previously overlooked (Whitney and Alvarez 1998). The approximate locations of territories in edge habitats, primary forest, and in or around treefall gaps were mapped, with reference to a surveyed trail system that effectively covered the local terrain. Antbird songs were recorded for species identification purposes, for subsequent analysis and preparation of sonograms, and for playback experiments both to locate conspecifics and to test for the possibility of interspecific responses to song playback. In April–May, antbird singing was consistent in several territorial species, but rather sporadic in others, limited to one or two repetitions of the song at dawn. Although the taping and playback of songs assisted in locating territories, it did not overcome problems of small sample sizes of territories in some of the rarer antbird species at the site.

The vegetation characteristics of located territories were measured. Vegetation density was recorded as the inverse of horizontal distance to 50% cover of an imaginary board in the vertical plane at a series of height (m) intervals: 0.15, 0.3, 0.6, 1.2, 2, 3, 4.5, 6, 7.5, 9, 10.5, and 15 m, and the approximate canopy height at the territory center was noted.

Antbird foraging behavior and ecology was

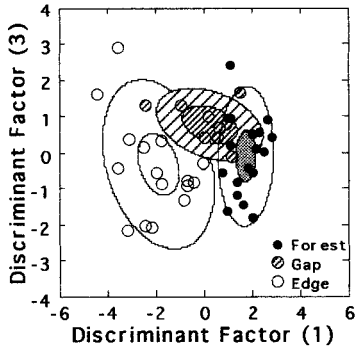

FIGURE 1. Discriminant function analysis of the vegetation characteristics in the territories of eight species of antbirds. Taller habitat is represented to right on the abscissa, vegetation more open at intermediate heights ranks higher on the ordinate. Forest interior species are distributed to the right (two species; n = 18 territories), Edge antbirds are positioned to the left (four species; n = 18 territories), and gap species (two species; n = 10 territories) are intermediate. Inner ellipses are 95% confidence ellipses for the means of each guild, outer ellipses 75% confidence ellipses for the three distributions.

observed and recorded, and foraging heights of the various species were assigned to the same set of height intervals described above. Information on body weights is taken from Stiles and Skutch (1989) and Dunning (1993).

STATISTICAL ANALYSES

Measurements of vegetation density were used to compute the relative amounts of vegetation within vertically-stacked horizontal layers, and these values were then used in discriminant function analyses (Systat 1992) to quantify interspecific differences in habitat use or preference.

Analysis of bird body weights within guilds was conducted in three ways. First, the range of weights (heaviest minus lightest species within a guild of n member species) was contrasted to null hypotheses by simulation. The distribution of the null (expected) range was generated from a random draw of size n, replicated 8,000 times, from the log(weight) distribution of the 20 lowland antbirds known to occur in southeastern Nicaragua. The observed ranges were then assigned a probability of occurrence based on the null distribution generated. Second, n intervals (on a log scale) were computed from n + 1 random draws, and the difference between the largest and smallest computed. The distribution of these differences was used as a null model to which the observed weight intervals were contrasted. The procedure again assigned a probability to the observations, the one-tailed test assessing the likelihood that the observed spacing of species on the log(weight) axis could be the result of a random selection of species' body weights. Third, the Barton-David test for uniform spacing of species along the body weight axis was used (Barton and David 1956). I computed the test statistic $[1-\Pr(G_{rs} < a)]$, the probability that the magnitude of the ratio of intervals r, s on the log(weight) scale (with ratios size-ordered 1, 2, 3, . . . , r, . . . , s, . . .) might be observed as high as a by chance alone. For a given number of n intervals measured after a random selection of (n + 1) points, $\Pr(G_{rs} < a)$ is computed as

$$a\binom{n}{s}\binom{s}{r+1}r(r+1)\sum_{i=0}^{r-1}\sum_{j=0}^{s-r-1}(-1)^{i+j}\binom{r-1}{i}\times\binom{s-r-1}{j}\times[(n-s+j+1)\times\{(s-r+i-j)a+(n-s+j+1)\}]^{-1}$$

for all $n(n+1)/2$ ratios of r, s resulting from the n intervals.

RESULTS

Of the 23 antbird species recorded for Nicaragua, 20 are expected to occur in the forested Caribbean lowlands (Table 1) and 3 to be restricted to higher-elevation forests of the interior. Nineteen of these 20 lowland species were seen at the study site, all except the habitual army-ant follower Spotted Antbird (scientific names listed in Table 1).

HABITAT PREFERENCES

The approximate locations of 48 territories of 12 species were found and plotted on a site map. Four species were found only in forest edge locations, four were forest interior species that shun the edge, and three others were found in or near treefall gaps within the forest (Table 1). These differences are reflected in vegetation measured within the territories.

Figure 1 shows results of the discriminant function analysis for representative species of different habitats for which adequate samples

TABLE 1. Species, guilds, and body weights of lowland forest antbirds in southeast Nicaragua. Sample sizes are given for territories and for foraging height observations in the two separate years of the study.

Guild	Species	Wt (g)	Territories			Foraging height		
			1994	1999	Total	1994	1999	Total
Edge	Great Antshrike *Taraba major*	67.5	3	3	6	15	8	23
	Barred Antshrike *Thamnophilus doliatus*	28.0	4	3	7	17	12	29
	Dusky Antbird *Cercomacra tyrannina*	16.3	2	1	3	43	12	55
Gaps	Fulvous-breasted Antpitta *Hylopezus fulviventris*	41.0	0	2	2	4	9	13
	Chestnut-backed Antbird *Myrmeciza exsul*	26.5	3	4	7	59	42	101
	Fasciated Antshrike *Cymbilaimus lineatus*	34.7	0	3	3	4	27	31
	Bare-crowned Antbird *Gymnocichla nudiceps*	30.6				30	5	35
Forest	Spectacled Antpitta *Hylopezus perspicillatus*	43.0	1	0	1	8	0	8
	Black-faced Antthrush *Formicarius analis*	62.2	4	5	9	19	14	33
	Slaty Antshrike *Thamnophilus atrinucha*	23.6	5	4	9	40	32	72
	Bare-crowned Antbird *Gymnocichla nudiceps*	30.6				30	5	35
	Wing-banded Antbird *Myrmornis torquata*	48.0	1	0	1	6	0	6
Army ant followers	Ocellated Antbird *Phaenostictus mcleannani*	51.1				4	12	16
	Bicolored Antbird *Gymnopithys leucaspis*	31.1				8	19	37
	(Spotted Antbird) *Hylophylax naevioides*	17.8						
Mixed-species flocks	Russet Antshrike *Thamnistes anabatinus*	20.7				0	6	6
	Dot-winged Antwren *Microrhopias quixensis*	7.9				0	59	59
	White-flanked Antwren *Myrmotherula axillaris*	8.4				0	13	13
	Streak-crowned Antvireo *Dysithamnus striaticeps*	17.0				0	47	47
	Plain Antvireo *Dysithamnus mentalis*	12.8				0	16	16
	Checker-throated Antwren *Myrmotherula fulviventris*	10.4				0	5	5
	(Tawny-crowned Greenlet) *Hylophilus ochraceiceps*					0	24	24
	(Lesser Greenlet) *Hylophilus decurtatus*					0	4	4

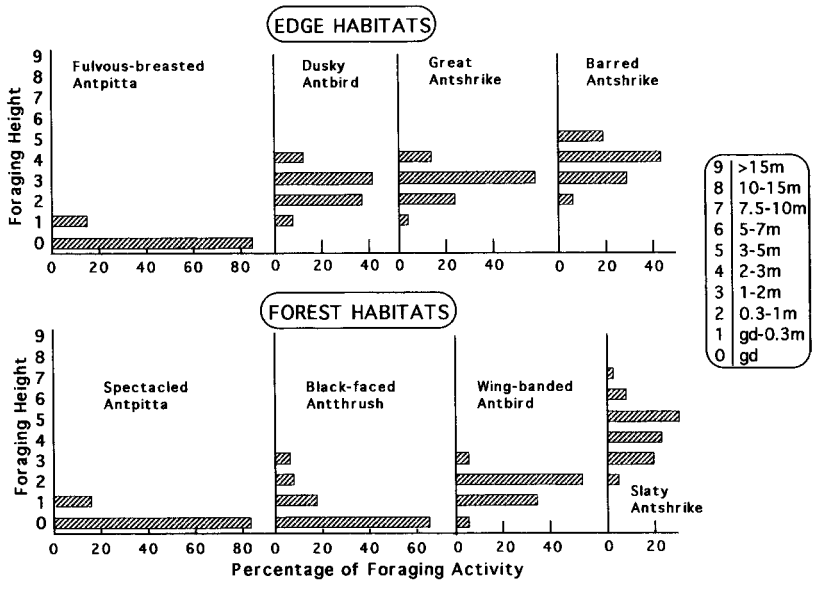

FIGURE 2. Foraging height distributions for species of the Edge and Forest guilds. Each foraging height observation (see Table 1 for sample sizes) is ≤60 sec in length; totals are 120 observations for Edge species and 154 for Forest species. All Forest species are significantly different in foraging heights (by χ^2 test, $P < 0.05$); all Edge species are significantly different except for Dusky Antbird and Great Antshrike ($P > 0.05$).

were collected. High canopy levels typical of forest habitats rank to the right on DF1, corresponding to the positions of forest species Black-faced Antthrush and Slaty Antshrike. Edge habitats typical of Great and Barred Antshrikes (n = 18) rank to the left on DF1, with Gap species Chestnut-backed Antbird and Fasciated Antshrike occupying an intermediate position. The Gap species rank higher on DF3, where higher values represent dense vegetation at low heights (1–3 m) but open at intermediate heights (3–6 m). Note that the means of each guild do not overlap, although the overall distributions do.

Three additional species not represented in Figure 1 share similar habitats. Bare-crowned Antbird is apparently a generalist species seen in gaps, occasionally in tall forest, and once attending army ant swarms. In two other species seen only in tall, closed forest, Spectacled Antpitta and Wing-banded Antbird, sample sizes were inadequate for their inclusion in the discriminant function analysis. Collectively, these conspicuously territorial species are segregated by habitat type, into Edge species, Gap species, and Forest species, with guild representation augmented by the rarer species as indicated in Table 1.

OTHER ANTBIRD LIFE-STYLES

Only antbird species that forage independently as pairs and sing vigorously on fixed territories are represented in Figure 1. Two other groups of antbirds occur at the site: (1) species which follow army ant swarms, and (2) species that associate in mixed-species flocks in the understory to subcanopy levels. Species in these guilds were generally distributed throughout the forest, and their territories (if they exist) were not plotted on the site map nor recorded relative to vegetation profiles.

These remaining antbird species at the site can unambiguously be assigned to the guilds "Army Ant Followers" and "Mixed-species Flocks" as follows. Ocellated Antbird and Bicolored Antbird were found only at ant swarms, and are apparently habitual army ant followers. Spotted Antbird (not encountered) also is known as an obligate army ant follower (Willis 1972), and is included here in the ant-following guild. The largest guild, numerically, is that of the subcanopy mixed-species flocks, with six antbird species (three antwrens, two antvireos, and an antshrike) and the fairly regular addition of two other small foliage insectivores, Tawny-crowned and Lesser Greenlets (Table 1).

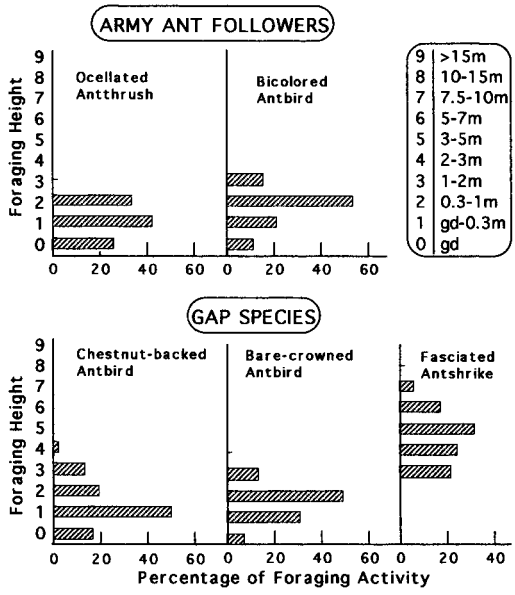

FIGURE 3. Foraging height distributions for species of the Gap and Army Ant guilds. Each foraging height observation (see Table 1 for sample sizes) is ≤60 sec in length; totals are 167 observations for Gap species and 53 for Army-ant followers. All species within guilds are significantly different in foraging heights (by χ^2 test, $P < 0.05$).

FORAGING HEIGHTS

Within guilds and associated habitats, there are significant differences among species in foraging heights (Figs. 2–4), with two exceptions: Dusky Antbird and Great Antshrike of the Edge guild, and Plain Antvireo and White-flanked Antwren in the Mixed-species Flocks are not significantly dissimilar (χ^2, $P > 0.05$). Foraging height differences are most conspicuous in Forest and Gap guilds, and least pronounced in the Mixed-species Flocks (Figs. 2–4).

SEGREGATION BY BODY SIZE

Antbirds vary dramatically among species by body weight (Table 1), with the Nicaraguan lowland species spanning nearly an order of magnitude. Within several of the guilds there is a clear segregation of species by body weight, more apparent in Edge and Army Ant guilds, less strikingly regular in the Forest and Mixed-flock guilds (Fig. 5). Gap antbirds are represented by three species of relatively similar weight. The generalist Bare-crowned Antbird is represented in Figure 5 in two guilds, Gap and Forest; it has not been included in the Army Ant guild because of its very irregular presence in that group.

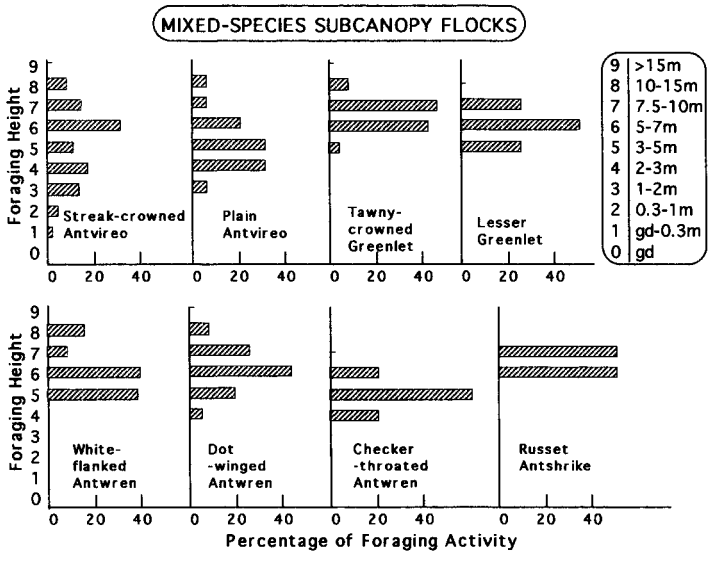

FIGURE 4. Foraging height distributions for eight species (six antbirds) of the Mixed-species flock guild. Each foraging height observation (see Table 1 for sample sizes) is ≤60 sec in length; totals are 174 observations for all species, but just 6 for Russet Antshrike, 5 for Checker-throated Antwren, and 4 for Lesser Greenlet. Among the remaining five species with large sample sizes, all pairwise comparisons show significant differences in foraging heights (by χ^2 test, $P < 0.05$) except for Plain Antvireo and White-flanked Antwren ($P > 0.05$).

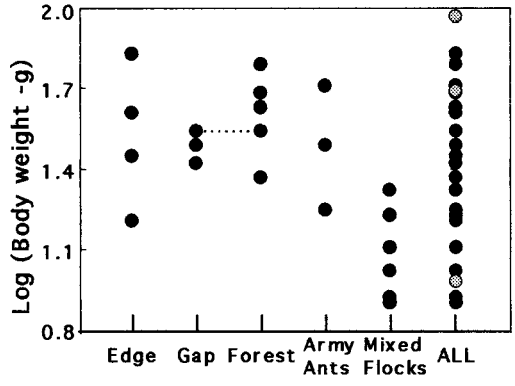

FIGURE 5. Distribution of log (body weight) for all 23 species of Nicaraguan antbirds (right, "ALL"), with 20 lowland species (solid dots) and 3 upland species (shaded dots) represented. Body weights of species in each of five guilds of antbirds are shown, in which even spacing among species within some guilds is apparent. Weight duplicates and a dual species listing (dotted line; Bare-faced Antbird) are discussed in the text.

To test body weight patterns, I first contrasted the observed weight range exhibited by guilds of size n species to the distributions of expected ranges of a random sample of size n from the distribution of lowland Nicaraguan antbird weights (as in Fig. 5, ALL). No significant differences were observed in four guilds ($P > 0.05$). In the fifth, the three Gap species display a (log) weight range of 0.12; $P = 0.05$ that a range this small would be generated by a random draw of three species from the $n = 20$ species pool.

Second, the expected distributions of differences between maximum and minimum body-weight intervals, computed from random draws, are plotted in Figure 6, for $n = 2$–5 intervals (corresponding to guilds of 3–6 species) and 8,000 replications. Observed differences between maximum and minimum intervals are significantly lower than expected ($P < 0.05$) in three guilds, Gap, Edge, and Mixed-flock species, permitting the conclusion that species in these guilds are non-randomly spaced in terms of log(body weight). In the remaining two guilds of Forest and Army Ant species, uniform spacing of species on the log(body weight) axis also is strongly suggested, with $P = 0.05$ and $P = 0.07$, respectively.

Third, the Barton-David test was applied to all $n(n + 1)/2$ ratios of intervals on the log(body weight) axis generated by $n + 1$ guild members. To illustrate the test procedure, consider a point dropped at random onto a line of unit length to divide it into two intervals summing to unity. The point drops by chance between 0.475 and 0.525 with probability 0.05, generating a ratio of intervals that is at least 0.475/0.525 = 0.905 in magnitude. The probability that the random point falls between 0.4 and 0.6 is 0.2, generating a ratio of intervals at least 0.667 in magnitude. Such probabilities are plotted as the ordinates in Figure 7, and descending lines show the decreasing probability of obtaining a ratio of at least the magnitude represented on the abscissa by chance alone.

Applying this test in Figure 7a, a single curve represents the null hypothesis for the two, 3-species guilds of Army Ant followers and Gap species. The two data points on this curve show the observed ratios in the two guilds; these observed ratios have probability 0.06 (Ant-followers) and 0.08 (Gap species) of chance occurrence. The 4-species guild of Edge species also is represented in Figure 7a, with three curves corresponding to the ratios of intervals 1:2, 1:3, and 2:3 (where intervals are ranked by size 1–3). Observed ratios (solid dots) are expected to occur by chance with probabilities 0.05, 0.007, and 0.09, respectively. The spacing by weight of the five Forest species is tested in Figure 7b. Of the six ratio tests permitted by five species and four intervals, only one returns a probability of occurrence <0.05 (namely $P = 0.04$ for $[1-\Pr\{G_{24}\}]$).

In some two dozen observations of mixed-species flocks, all contained either Dot-winged Antwren (log[wt] = 0.90) or White-flanked Antwren (log[wt] = 0.92), with about equal frequency, but none contained both species. As these "size duplicates" were not observed in the same flock, the Mixed-species flocks are divided into two sub-guilds, those with Dot-winged Antwren and those with White-flanked Antwren. Interval ratios are tested for the two flock types separately in Figure 7c. As the figure indicates, 9 of 12 ratios are of a magnitude large enough to be expected to occur by chance with $P < 0.05$, indicating significantly even-size spacing. In contrast, if the six Mixed-flock species are tested as a single guild, just 3 of 10 ratios are significant. Thus, of the 23 ratios tested in Figure 7, 12 indicate significantly even spacing of species by body weight at the $P < 0.05$ level, and a further 4 at the $P < 0.10$ level. Of the

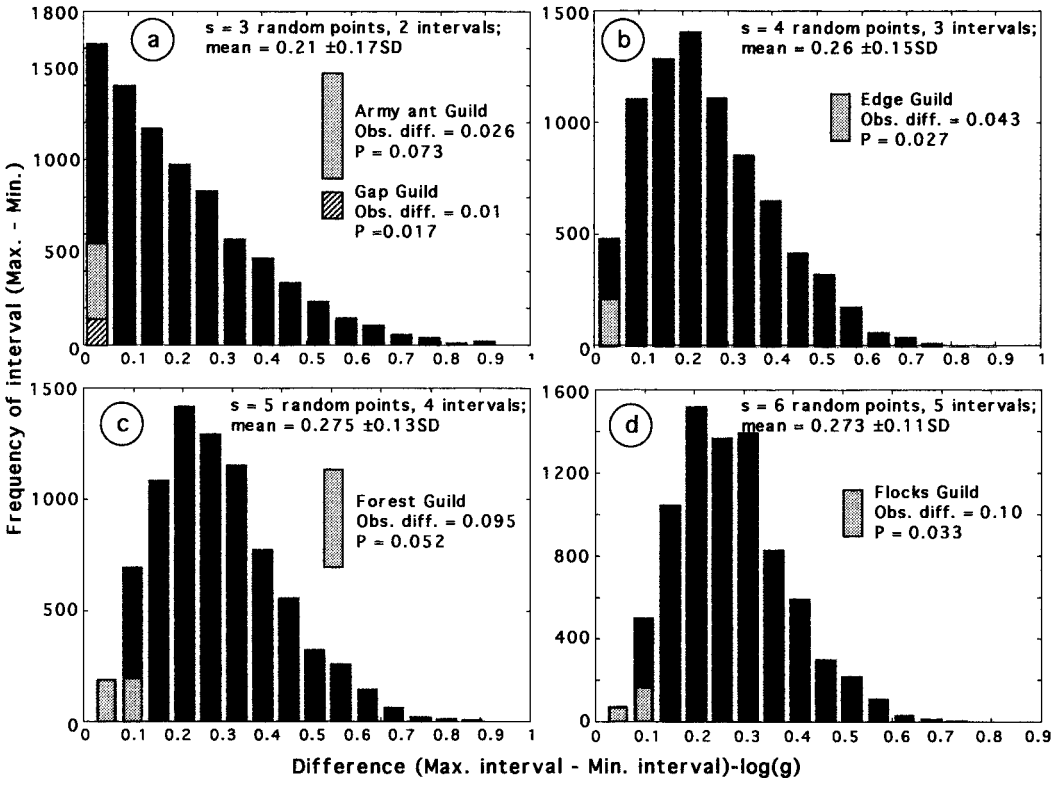

FIGURE 6. Simulated frequency distributions of the difference between maximum and minimum intervals generated by random selection of species' samples from the antbird body-weight distribution. Distributions simulate (a) 3-species guilds, (b) 4-species guilds, (c) 5-species guilds, and (d) 6-species guilds. Stippled and hatched areas to the lower left indicate where observations of actual (observed) differences lie in the antbird guilds of different weights.

seven remaining ratios with $P > 0.10$, four come from the Forest guild, in which the hypothesis of regular spacing of species by weight is unsupported.

Beyond these tests of body-weight differences within guilds, further perspective on weight segregation is obtained by examination of species with similar body weight but members of different guilds. For example, five antbirds occur in the weight range 17.8–28 g, log(wt) = 1.25–1.45, and all are members of different guilds: Spotted Antbird (log[wt] 1.25) follows ants, Russet Antshrike (log[wt] 1.32) forages in mixed-species flocks, Slaty Antshrike (log[wt] 1.37) is a forest species, Chestnut-backed Antbird (log[wt] 1.42) a gap species, and Barred Antshrike (log[wt] 1.45) an edge species. Similarly, the four species between log(wt) 1.49 and 1.63 also are all in different guilds. There are two 31-g species: Bicolored Antbird, which habitually follows ant swarms, and Bare-crowned Antbird, which is most commonly associated with gaps. The two antpittas are of very similar weight (41–43 g), but Spectacled Antpitta is a forest interior species and Fulvous-bellied Antpitta occurs only in forest-edge habitats. This segregation of species with similar body weight into different guilds produces a pattern complimentary to that of different weights within guilds.

Regularity of weight differences within guilds occurs despite variation among guilds in the factors by which species differ in weight. Weight differences are large in Edge and Army Ant guilds, where species differ by weight factors of 1.74 and 1.71, respectively, but are considerably smaller in Mixed-species flocks (factor 1.27) and in Gap species (factor 1.15). In the Forest guild, where regularity in weight spacing is not supported, the size factor averages 1.27.

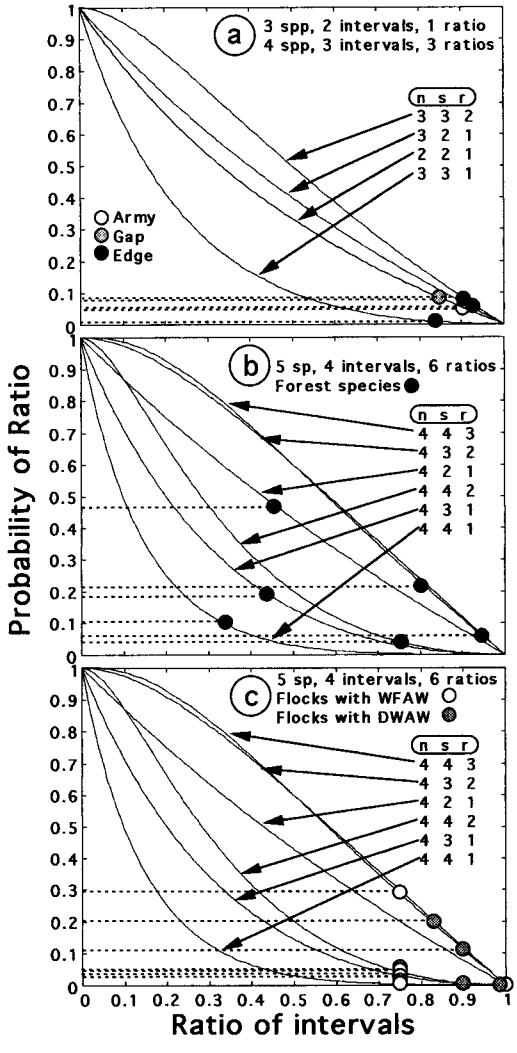

FIGURE 7. Barton-David test results for expected probabilities of interval ratios: (a) for 3-species and 4-species guilds, (b) for the 5-species forest guild, and (c) the two alternative five-species guilds representing mixed-species flocks, those with White-flanked Antwren (WFAW) versus Dot-winged Antwren (DWAW). Actual observed ratios are indicated with the dots (solid, open, or shaded), and their corresponding probabilities under the null hypothesis of random spacing are shown by dotted lines extending to the ordinate.

BODY WEIGHT AND FORAGING HEIGHT SEGREGATION

Ecological segregation within antbird guilds may be enhanced by interspecific differences on both body weight and foraging height. There appears to be complementarity between these two niche axes. For example, there is strong segregation by foraging height among Gap species (Fig. 3; average 33% overlap), which are relatively similar in body weights. On the other hand, the Edge species are well segregated by body weights (Fig. 5), although three of the four show substantial overlaps in their foraging height distributions, and overlap is highest (82.5%) in the two species most dissimilar in weight (Great Antshrike and Dusky Antbird; Fig. 2). Ant followers also show strong weight segregation but extensive (average 58%) foraging height overlap. In the Forest species, statistical significance of regularity in weight segregation is precluded by the close similarity in Spectacled Antpitta (43 g) and Wing-banded Antbird (48 g), but these two species have scarcely any overlap in foraging heights (Fig. 3). And lastly, the two antwrens with similar weights that occurred in different flocks are also the two Mixed-flock antbirds with the most similar foraging height distributions (Fig. 4, lower left).

It might be suspected that body weights are related to the vegetation structure encountered by foraging antbirds, and that the segregation of antbird body weights over foraging height is perhaps regulated by vegetation density. For example, body weight is narrowly constrained among the Edge species that all occupy the very dense, edge vegetation. However, tests on the relationship for the six territorial species for which vegetation profiles were measured reveal no significant patterns. The relation between foraging height, body weight, and vegetation density is clearly a complex one, and requires further data and analysis.

DISCUSSION

A range of ecological, behavioral, and morphological differences serve to distinguish among the approximately 20 species of coexisting antbirds in and around lowland primary forests of the Caribbean slope. Species can be readily assorted into distinct guilds based on a combination of the habitats they occupy (three guilds: Edge, Gap, and Forest) and the foraging strategies they employ (two guilds: Mixed-species flocks and Ant-following species).

Within several guilds, species are strikingly different in body weights, which form regularly spaced series on a logarithmic axis. However, weight ratios differ among guilds, and it is by no means clear what controls these inter-guild

differences in body-weight ratios. They may be related to differences in prey body sizes, but if so this simply begs the question as to why species should tolerate more potential prey-size overlap in mixed-species flocks than in edge habitats. Willis and Oniki (1978) have shown that species attending army-ant swarms have relatively fixed foraging site positions, with larger species lower and more central and smaller species higher and more peripheral to the swarms. Such microsite differences among species in part may determine body weight in the different swarm attendants. In edge, gap, and forest-interior species, there are striking differences in foraging heights, which in general covary with differences in vegetation structure. It might well be that differences in vegetation density, with a very general association between smaller body weight and denser vegetation, are contributing factors to body weight beyond those of specialization on prey of different sizes.

Previous studies of antwren flocks have shown that component species differ in their location of territories, preferred foraging sites such as vine tangles vs. open foliage, and foraging methods, and that flock composition is regulated by both intraspecific and interspecific agonistic interactions (Jones 1977, Gradwohl and Greenberg 1980). These species clearly differ ecologically in more ways than those inferred from modest differences in body weight and feeding heights. In my study, mixed-species flocks with Dot-winged versus White-flanked Antwren flocks appeared to occur throughout the forest in mosaic fashion. Although not quantified, their apparent segregation may be due to habitat differences between the two species, or to direct behavior interactions between them that preclude their foraging together in the same flock.

Given the patterns in antbird species assemblages described here, it would be interesting to examine how they are changed or augmented when the number of locally coexisting species is doubled, as in some parts of Amazonia, or halved, as for example in the Isthmus of Tehuantepec region of Mexico. There are ample opportunities in this group for a great deal of further research, including work on diet, foraging ecology and behavior, habitat selection, and both direct and indirect interspecific interactions.

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