

DIVERSITY OF BIRDS ALONG AN ELEVATIONAL GRADIENT IN THE CORDILLERA CENTRAL, COSTA RICA

JOHN G. BLAKE¹ AND BETTE A. LOISELLE

Department of Biology and International Center for Tropical Ecology, University of Missouri–St. Louis, St. Louis, Missouri 63121, USA

ABSTRACT.—Species diversity and community composition of birds change rapidly along elevational gradients in Costa Rica. Such changes are of interest ecologically and illustrate the value of protecting continuous gradients of forest. We used mist nets and point counts to sample birds along an elevational gradient on the northeastern Caribbean slope of the Cordillera Central in Costa Rica. Sites included mature tropical wet forest (50 m); tropical wet, cool transition forest (500 m); tropical premontane rain forest (1,000 m); and tropical lower montane rain forest (1,500 and 2,000 m). We recorded 261 species from 40 families, including 168 species captured in mist nets (7,312 captures) and 226 detected during point counts (17,071 observations). The sample included 40 threatened species, 56 elevational migrants, and 22 latitudinal migrants. Species richness (based on rarefaction analyses) changed little from 50 to 1,000 m but was lower at 1,500 and 2,000 m. Mist nets and point counts often provided similar views of community structure among sites based on relative importance of difference categories of species (e.g. migrant status, trophic status). Nonetheless, important differences existed in numbers and types of species represented by the two methods. Ninety-three species were detected on point counts only and 35 were captured only. Ten families, including ecologically important ones such as Psittacidae and Cotingidae, were not represented by captures. Elevational migrants and threatened species occurred throughout the gradient, illustrating the need to protect forest at all elevations. A comparable study from the Cordillera de Tilarán (Young et al. 1998) demonstrated similar patterns of species change along an elevational gradient. Comparisons with that study illustrated that point counts are a valuable complement to mist-net studies. Both studies indicated the diverse nature of the avifauna along elevational gradients in Costa Rica. *Received 8 December 1998, accepted 7 December 1999.*

COSTA RICA has a well-deserved reputation for conservation and biological diversity (Janzen 1983, Gamez and Ugalde 1988). Yet, outside of protected areas, much of the country has been deforested, making national parks and other reserves especially important for conservation of birds and other organisms. Costa Rica also has been the site of many studies on birds (at least 340 publications from 1979 to 1995; Winker 1998). Two areas have been the focus of many of these studies: Monteverde Cloud Forest Reserve and surrounding areas, and La Selva Biological Station and adjacent Braulio Carrillo National Park. Patterns of diversity of plants and animals along elevational gradients have been examined in both regions (Hartshorn 1983, Stiles 1983).

Early work by Oriens (1969) and Terborgh (1971) on elevational distribution patterns of birds in Costa Rica and Peru, respectively, stim-

ulated later studies on the roles of biotic (competition, resource abundance, vegetation structure) and abiotic (rainfall, temperature) factors on species distribution patterns and community structure in tropical forests (Beehler 1981, Loiselle and Blake 1991). Declines in bird-species richness with elevation are common, but important differences exist in the patterns of change among functional groups (i.e. foraging guilds, migrant status) of birds (e.g. Stiles 1983). Declines in species richness have been attributed to declines in forest area at higher elevations, declines in abundance and size distribution of invertebrates, competition, and changes in environmental conditions (Terborgh 1971, Beehler 1981, Janes 1994). Local migrations of birds along elevational gradients also are an important factor structuring bird assemblages and are a critical consideration in conservation efforts (Stiles 1988, Loiselle and Blake 1991, Winker et al. 1997).

Mature tropical forest extends from near sea level at La Selva south for about 35 km to more

¹ E-mail: blake@jinx.umsl.edu

than 2,900 m atop Volcán Barva on the Caribbean slope of the Cordillera Central. It is the last remaining gradient of continuous forest in Central America to extend over such an elevational range (Norman 1985). Life zones range from lowland tropical wet forest in La Selva and lower elevations within the park to montane rain forest at the volcano tops (Hartshorn and Peralta 1988). The fact that forest is protected along a continuous elevational gradient makes it particularly important for conservation (Stiles and Clark 1989), especially given that many species of birds make regular elevational migrations along this gradient (Stiles 1988) and that most lowland forest in the region has been cleared (Butterfield 1994).

We have conducted studies on birds along most of this gradient (from ca. 40 to 2,000 m), providing a unique opportunity to evaluate changes in bird diversity and turnover in species composition among elevations. Our studies also provide an opportunity to compare patterns of diversity between the Monteverde region of Cordillera de Tilarán, recently described by Young et al. (1998), and the La Selva/Volcán Barva region of the Cordillera Central (ca. 80 to 85 km apart). The studies at Monteverde spanned five life zones and illustrated the importance of the region for conservation and the spatial complexity of bird distribution patterns (i.e. distinctiveness of the avifauna in different life zones). Missing from that study, however, were data from lowland sites and from birds not readily captured in mist nets (e.g. many canopy birds). Our studies from La Selva and Braulio Carrillo include data from lowland habitats and are based on samples from mist nets and point counts. These two methods typically sample different but often complementary components of the avifauna. The major objectives of this paper are to: (1) describe avian diversity and turnover along a 2,000-m elevational gradient in Costa Rica, (2) determine structural changes in the avifauna that reflect variation in ecological functions of birds in forests at different elevations, and (3) discuss differences in diversity among life zones located within different montane regions of Costa Rica. In addition, we compare results obtained from mist nets with those obtained from point counts.

STUDY AREA

We conducted research at La Selva Biological Station, located in the lowlands of northeastern Costa Rica (10°25'N, 84°01'W) and adjacent Braulio Carrillo National Park. La Selva encompasses approximately 1,500 ha, of which about 67% is old-growth forest. Braulio Carrillo (ca. 45,000 ha) borders La Selva to the south; more than 75% of the corridor connecting La Selva to the main forest block of Braulio Carrillo is old-growth forest. Approximate elevations at our main study sites were 50 m at La Selva and 500 m, 1,000 m, 1,500 m, and 2,000 m in the park (Fig. 1). Forest life zones (Holdridge 1967) included tropical wet (50 m); tropical wet, cool transition (500 m); tropical premontane rain (1,000 m); and tropical lower montane rain (1,500 m and 2,000 m; Hartshorn and Peralta 1988). Approximate distances between study sites were 10 km (50 to 500 m), 6 km (500 to 1,000 m), 5 km (1,000 to 1,500 m), and 7 km (1,500 to 2,000 m). We typically refer to forest types by elevation but note that they correspond to different and relatively distinct life zones (except the sites at 1,500 m and 2,000 m).

All sites were located in old-growth forest. Canopy heights were approximately 30 to 40 m at 50 m elevation, 35 to 40 m at 500 m, 30 to 35 m at 1,000 m, 25 to 30 m at 1,500 m, and 20 m at 2,000 m (Hartshorn and Peralta 1988). Numbers of tree species (trees >10 cm dbh in 1-ha plots; Lieberman et al. 1996) were 115 species at 100 m; 131 species at 500 m; 100 species at 1,000 m; 74 species at 1,500 m; and 55 species at 2,000 m. The composition of tree species changed continuously along the gradient with no discrete breaks (Lieberman et al. 1996).

La Selva receives approximately 4,000 mm of rain annually. The dry season typically lasts from late January or early February to March or April, with a second, less-pronounced dry season in September and October. Although few climatic data are available from higher elevations along the La Selva-Volcán Barva transect, rainfall probably is highest between 1,000 and 1,500 m. Hartshorn and Peralta (1988) reported mean annual rainfall ranging from 3,268 mm at 2,260 m elevation to 5,096 at 970 m in areas adjacent to the transect along which we worked. The seasonal pattern of rainfall in Braulio Carrillo is similar to that at La Selva, but the dry season is shorter and less pronounced. Rain or mist and clouds occur almost daily at high elevations.

METHODS

Mist nets.—We sampled birds with mist nets and point counts (see below). Mist-net studies started in La Selva in 1985 and continued until 1994. Studies in Braulio Carrillo started in 1985 and continued through 1989. Most data were collected during December to April (late wet season, dry season, to early



FIG. 1. Study sites in La Selva Biological Station and Braulio Carrillo National Park, Costa Rica. Elevations represent tropical wet forest (50 m); tropical wet, cool transition forest (500 m); tropical premontane forest (1,000 m); and tropical lower montane forest (1,500 to 2,000 m).

wet season), although netting was conducted throughout 1985 (Blake and Loiselle 1991, Loiselle and Blake 1991). We used mist nets at ground level (12 m × 2.8 m, 36-mm mesh) to sample birds occurring in undergrowth of mature forest at 50 m, 500 m, and 1,000 m. Rain and mist were too frequent at 1,500 and 2,000 m to justify use of nets. Nets were located 40 m apart on a 10-ha grid in one tropical wet forest site at about 50 m. At all other sites, nets were set approximately 40 m apart along narrow trails or in lines cut in the forest undergrowth. Area covered was approximately 5 to 8 ha at each site. Net locations were random with respect to topography, locations of fruiting plants, treefall gaps, or other factors that might influence capture rates (i.e. we did not select net sites based on a subjective assessment

of capture probabilities). Nets typically were operated from dawn to about 1300 at 50 m and until dusk at higher elevations. Nets at a given site were operated for two days (sometimes three days depending on rain) during each sample period. We conducted 28 sample periods across 10 years at the main lowland (50 m) forest site, 5 sample periods in two years at the second lowland site, and 17 sample periods across 5 years at the 500 m and 1,000 m sites.

Mist nets are subject to several biases, especially if used to estimate abundance (Remsen and Good 1996). Nets are, however, an effective way to gather data on birds that occur in the understory (Karr et al. 1990, Blake and Loiselle 1991). Young et al. (1998) provide a thorough discussion on the use of netting data for analyses such as ours; their conclusions ap-

ply equally to our study, and the reader is referred to their paper for details. We avoided some of the potential problems discussed by Young et al. because we used the same type of mist net for all of our studies, and all samples were collected from old-growth forest.

Point counts.—We also sampled birds with point counts (10 min per count) in tropical wet forest at La Selva (two sites) and at 500, 1,000, 1,500, and 2,000 m in Braulio Carrillo. At least 8 points were established at each site. Points were approximately 200 m apart and were centered on the same areas where netting was conducted (at sites from 50 to 1,000 m) or were along narrow preexisting trails at 1,500 and 2,000 m. Point counts covered more area than nets but did not include more than one habitat. Counts were conducted from 1987 to 1994 at one site in La Selva and during 1988 and 1989 at all remaining sites. All points were sampled on two to four days during two to three periods per year (ca. 5 to 6 weeks apart) at all sites during 1988 and 1989. Counts started approximately 20 min before dawn and continued for no more than 2 h past dawn (Blake 1992). All birds seen or heard were noted.

Detections of birds during point counts are influenced by many factors (behavior of species, characteristics of vegetation, weather conditions, observer, etc.; Blake 1992, Ralph et al. 1995). If elevational gradients existed in detection probabilities, then differences in results among elevations might simply reflect differences in detection. We have no reasons to suspect that such a gradient exists. All counts were conducted by the authors, both of whom are extremely familiar with the vocalizations and plumages of birds in Costa Rica. We reduced the importance of environmental factors by counting only on days with little or no wind or rain; occasional mist at higher elevations was unavoidable. We encountered mixed-species flocks more frequently in Braulio Carrillo, and their presence might influence results because of difficulties in counting or detecting all birds in a flock. We feel this potential problem was minimized because of the number of counts conducted, only two people conducted counts (reducing any observer differences), and accumulation curves for observational data approached an asymptote at higher elevations.

Analyses.—In general, we followed Young et al. (1998) in analyzing patterns of species diversity and faunal turnover to facilitate comparisons with their study (hereafter Young et al.). Sample effort varied among sites in both studies. Thus, we did not make comparisons based on capture rates or mean numbers per point but instead used either presence/absence of species or proportions. All captured birds were banded with numbered aluminum bands, but individuals could not be distinguished during counts. Thus, we used total captures (including re-

captures) and total observations (which likely include resightings) in all comparisons.

We calculated an estimate of beta (β) diversity (diversity across elevations or life zones; Schluter and Ricklefs 1993) as:

$$\beta = \gamma/\alpha n, \quad (1)$$

where γ is the gamma diversity (total number of species), α is the average number of species per life zone, and n is the number of life zones. We calculated a separate beta diversity from netting and observation data. In addition, following Young et al., we calculated Jaccard's similarity matrix based on presence/absence of species. We used nonmetric multidimensional scaling (McCune and Mefford 1995) to graphically compare the similarity in species composition among different habitats. Numbers of individuals captured or counted per species were relativized (general relativization by row and column totals; McCune and Mefford 1995) prior to analyses. We used a Monte Carlo permutation procedure to determine if the information extracted by the axes was more than expected by chance (i.e. whether the reduction in stress associated with each axis was significant). A similar procedure was used to compare similarity among habitats based on trophic groups (see below). We used Mantel tests (McCune and Mefford 1995) to compare correlations among similarity matrices; 1,000 permutations were run to determine the significance of the observed correlations.

Numbers of individuals captured or detected differed among sites, precluding direct comparisons of species numbers. Instead, we calculated rarefaction curves using Monte Carlo simulation (EcoSim version 1.11; Gotelli and Entsminger 1997) that allows comparison of the number of species expected per site based on the lowest number of individuals recorded among sites being compared; i.e. species richness is compared based on the same number of individuals. Simulations were run 1,000 times, and mean expected numbers of species at each site were compared based on the 95% CI (nonoverlapping CIs indicate a significant difference in means).

We assigned species to migratory categories (latitudinal [long-distance] migrant, elevational migrant) based on AOU (1998), Stiles and Skutch (1989), and personal observations. We further assigned species to trophic groups based on primary foraging substrate and food type; assignments were based on analyses of fecal samples, observations of foraging behavior, and the literature (e.g. Stiles and Skutch 1989). We followed Young et al. in using Parker et al. (1996) to assign conservation (threatened) status to species; all species listed as of medium or higher conservation concern were included. We also included species listed by Collar et al. (1994) as near threatened or vulnerable in Costa Rica and those listed by Stiles (1985) as endangered in Costa Rica. Data on body size are from Stiles and Skutch (1989).

TABLE 1. Number of captures and observations by elevation^a in the Cordillera Central, Costa Rica.

	50 m		500 m		1,000 m		1,500 m	2,000 m
	Capture	Observe	Capture	Observe	Capture	Observe	Observe	Observe
Captures or observations	4,029	8,803	1,733	2,182	1,550	2,159	2,097	1,830
Species	107	132	92	105	83	91	55	50
Species (captures and observations)		157		143		118		
Mist-net hours	20,633		4,825		5,587		22	22
Number of counts		70		12		15		

^a Tropical wet forest (50 m); tropical wet, cool transition forest (500 m); tropical premontane forest (1,000 m); tropical lower montane rain forest (1,500 and 2,000 m).

RESULTS

Species richness and composition.—We recorded 261 species (Table 1, Appendix 1), including 168 species captured in mist nets (7,312 captures) and 226 recorded during point counts (17,071 observations, excluding unidentified birds). Forty families were represented (excluding *incertae sedis* genera; Appendix 2). The total

included 40 threatened species, 56 elevational migrants, and 22 latitudinal (long-distance) migrants. Rarefaction curves indicated that some new species still were being captured at all sites (i.e. no indication of an asymptote; Fig. 2). In contrast, the rate at which new species still were being recorded during counts leveled off to a greater extent, particularly at 1,500 and 2,000 m. Number of species represented in 1,000 captures showed less variation from 50 to 1,000 m than did number of species represented in 1,000 observations (Fig. 3). Declines in species richness with elevation were evident from count data. Species numbers differed between netting and count data at 50 and 500 m, but not at 1,000 m.

Species composition differed among sites for both netting and count data. Beta diversity from 50 to 1,000 m was 0.60 and 0.61 based on netting and count data, respectively. Beta diversity across all five elevations (count data)

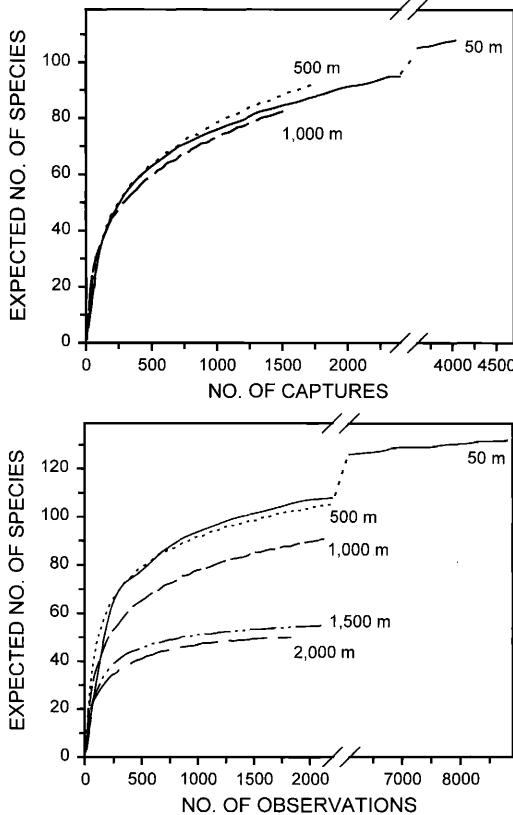


FIG. 2. Species rarefaction curves based on numbers of captures or numbers of observations.

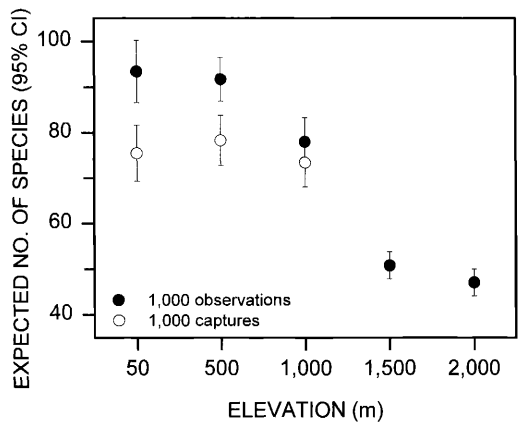


FIG. 3. Mean (and 95% CI) expected number of species (based on 1,000 simulations) in samples of 1,000 captures or 1,000 observations. Means are considered different if CIs do not overlap.

TABLE 2. Jaccard similarity indices based on species presence/absence and on proportion of individuals per species.

	Captures			Observations			
	50 m	500 m	1,000 m	50 m	500 m	1,000 m	1,500 m
Presence/absence							
Captures							
500 m	0.56						
1,000 m	0.20	0.28					
Observations							
50 m	0.52	0.37	0.14				
500 m	0.45	0.38	0.13	0.62			
1,000 m	0.14	0.17	0.48	0.19	0.17		
1,500 m	0.04	0.06	0.29	0.02	0.05	0.38	
2,000 m	0.02	0.02	0.16	0.01	0.01	0.18	0.50
Proportion of individuals per species							
Captures							
500 m	0.49						
1,000 m	0.07	0.10					
Observations							
50 m	0.12	0.09	0.03				
500 m	0.14	0.13	0.04	0.55			
1,000 m	0.02	0.05	0.25	0.03	0.05		
1,500 m	0.01	0.03	0.22	0.01	0.02	0.45	
2,000 m	0.00	0.01	0.08	0.00	0.00	0.16	0.25

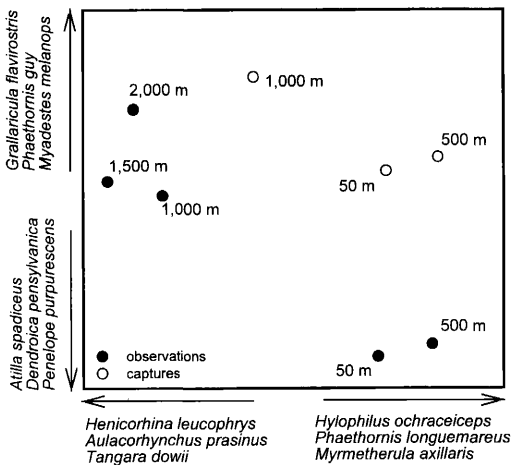


FIG. 4. Nonmetric multidimensional scaling ordination of study sites based on captures or observations. Distance between points indicates degree of similarity. The first axis largely represents a gradient in species composition from low to high elevations whereas the second axis largely reflects differences between species observed but not captured (and vice versa) in the two lower elevations.

was 0.52. Similarity among sites was relatively low based on species presence/absence, particularly for habitats that were farther apart (Table 2, Fig. 4). Similarity in species composition between netting and count data within sites ranged from 0.52 at 50 m to 0.38 at 500 m, indicating substantial differences in species recorded at a site by the two methods. Such differences were apparent in the ordination (Fig. 4). The first axis of the ordination largely separated sites on the basis of elevational gradients in species distributions, whereas the second axis largely reflected effects of species observed but not captured at 50 and 500 m (including many canopy species). Axes extracted significantly more information from the original data matrix than expected by chance ($P < 0.01$).

Although many species were recorded by netting and counts, the relative numbers of individuals per species recorded by the different methods often differed substantially, providing different perspectives on relative importance of individual species among and within sites (Appendix 1). Similarity among sites generally was lower than when based on presence/absence (Table 2).

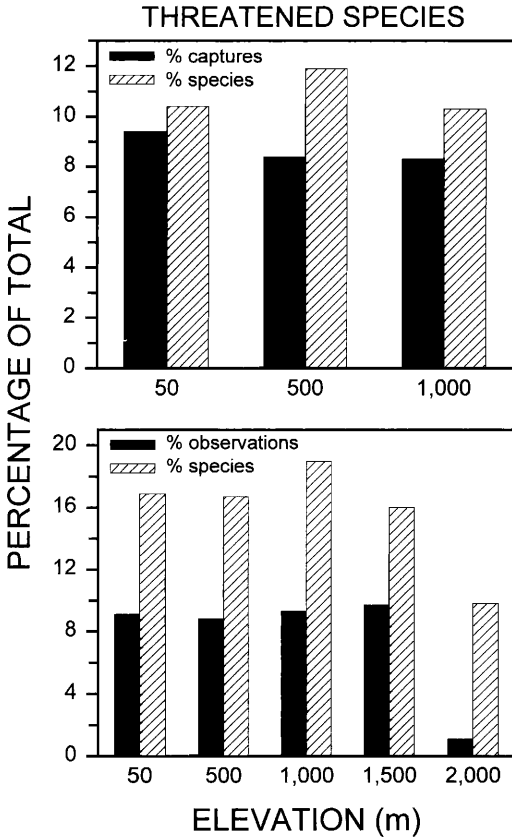


FIG. 5. Percentage of captured and observed species and individuals represented by threatened species.

Few species occurred in more than two or three life zones (Appendices 1 and 2). Only *Mionectes olivaceus* and *Myadestes melanops*, both elevational migrants, were recorded at all five sites. The number of species recorded at only one elevation ranged from 27 at 50 m (17% of the total from that elevation) to 2 at 1,500 m (4% of total); 30% of species at 2,000 m were not recorded at any other elevation. The mean number of zones per species (counting 1,500 m and 2,000 m as separate zones) was $1.6 \pm \text{SE of } 0.08$ across families based on netting data (three zones) and 1.8 ± 0.08 based on count data (five zones). The number of life zones per species was higher for count data than for netting data (paired *t*-test of families represented by count and netting data; $t = 3.17$, $df = 28$, $P < 0.01$). Furthermore, the mean number of zones per species was not correlated between netting and count data (i.e. comparing families represented

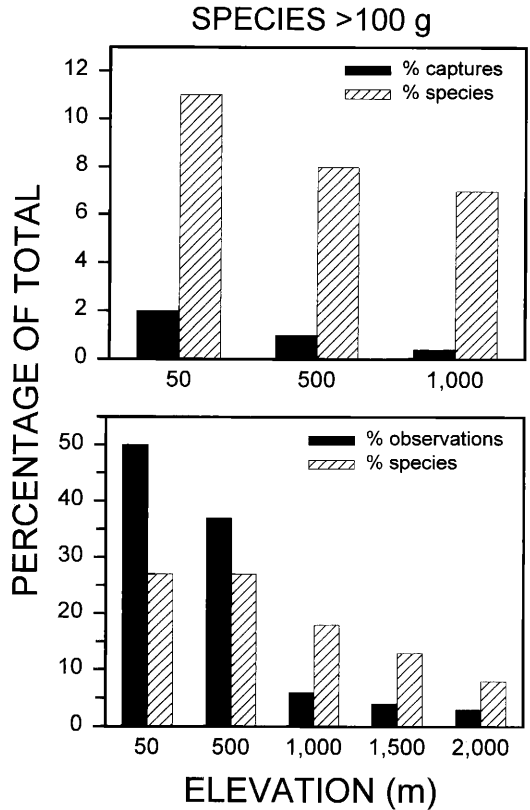


FIG. 6. Percentage of captured and observed species and individuals represented by large (>100 g) species.

by both netting and capture data; $r_s = 0.07$, $P > 0.50$).

Substantial differences occurred among elevations when comparisons were based on different groups. Threatened species accounted for about 10 to 12% of captured species and approximately 9 to 19% of observed species (Fig. 5). Threatened species were least important at 2,000 m. Distribution of threatened species numbers did not differ among zones based on netting versus count data ($\chi^2 = 0.20$, $df = 2$, $P > 0.90$), although threatened species made up a greater proportion of count data. The number of large (>100 g) species declined with elevation (Fig. 6). Large species made up a much larger proportion of count data than of netting data, but the distribution of numbers of large species did not differ among zones ($\chi^2 = 0.20$, $df = 2$, $P > 0.90$). The proportions of large species captured were higher than proportions of large individuals captured at all sites. The

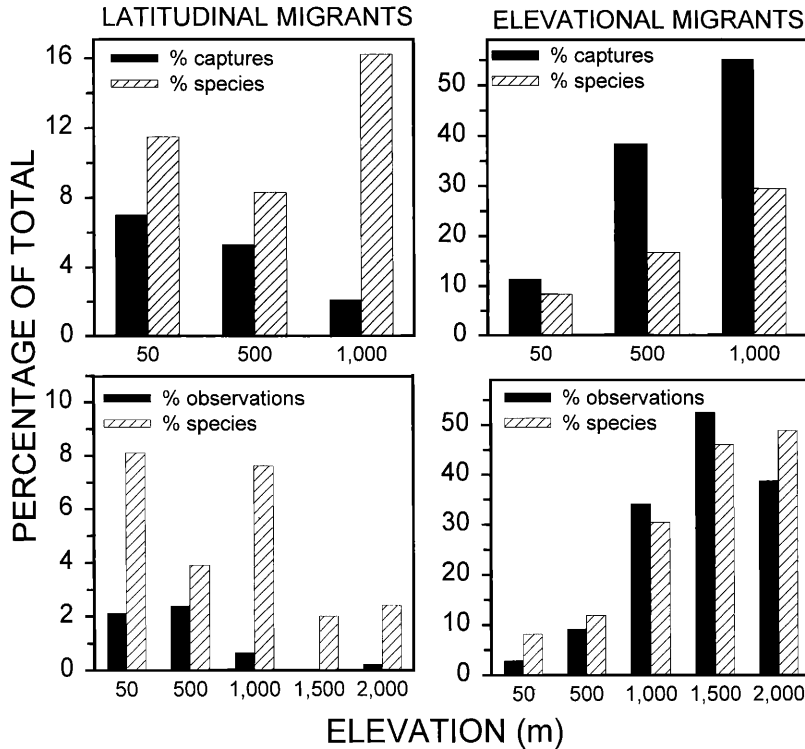


FIG. 7. Percentage of captured and observed species and individuals represented by latitudinal and elevational migrants.

same was true for count data at sites from 1,000 to 2,000 m, but the reverse was true for sites at 50 and 500 m.

Migrants.—Latitudinal migrants were less commonly observed and captured at higher elevations (Fig. 7). The proportional number of latitudinal migrant species was high at 50 m and 1,000 m based on both types of data but was low above 1,000 m (count data only). The relative distribution of latitudinal migrant species among elevations did not differ between netting and count data ($\chi^2 = 0.71$, $df = 2$, $P > 0.70$). Latitudinal migrants did, however, make up a greater proportion of species and individuals captured than observed at a given elevation (compare upper and lower left panels of Fig. 7). Elevational migrants (Fig. 7) comprised a high proportion of species and individuals at higher-elevation forests. Relative numbers of elevational migrant species among elevations were similar between netting and count data ($\chi^2 = 0.56$, $df = 2$, $P > 0.75$). Elevational migrants typically made up greater proportions of captures than observations. The distribution

of species in the two migrant categories (latitudinal vs. elevational) differed among sites for count data ($\chi^2 = 18.4$, $df = 4$, $P < 0.001$) but not for netting data ($\chi^2 = 3.5$, $df = 2$, $P < 0.20$).

Trophic groups.—The dominant trophic groups were arboreal frugivores, arboreal frugivore/insectivores, foliage insectivores, and nectarivore/insectivores (Table 3). Fewer groups were present in lower montane forest (1,500 and 2,000 m); epiphyte feeders generally were restricted to such forests. Netting and count data differed in proportional representation of individuals within some trophic groups (Table 3). Nectarivores (primarily trochilids), bark insectivores (primarily dendrocolaptids such as *Glyphorhynchus spirurus*), and army-ant followers (primarily thamnophilids) accounted for greater proportions of captures than observations; species representative of these groups typically forage at net levels. The reverse was true for foliage insectivores and arboreal frugivores, many of which forage above net levels, often in the canopy. Differences between netting and count data were less pro-

TABLE 3. Percentage of species and individuals in different trophic categories based on captures (Cap) and Observation (Obs); “+” indicates values <0.5%.

Trophic group	50 m		500 m		1,000 m		1,500 m	2,000 m
	Cap	Obs	Cap	Obs	Cap	Obs	Obs	Obs
Species per group								
Terrestrial frugivore	4	2	3	2			2	
Arboreal frugivore	8	17	10	15	6	16	18	18
Terrestrial frugivore/insectivore	3	3	1	3	1	1	4	6
Arboreal frugivore/insectivore	18	20	16	22	25	22	21	24
Ground insectivore	7	5	10	4	10	4	5	2
Foliage insectivore	26	25	26	27	24	24	16	18
Bark insectivore	6	8	3	8	6	7	7	4
Flycatching insectivore	5	3	4	2	5	3	5	6
Army-ant followers	5	4	4	5	1	1		
Nectarivore/insectivore	11	7	15	7	15	12	16	16
Granivore	2		3		2			
Carnivore	3	4	2	3	2	5		
Piscivore	1							
Epiphyte insectivore			1		2	2	7	8
Nectarivore/frugivore	2	1		2		1		
Individuals per group								
Terrestrial frugivore	1	1	1	+			+	
Arboreal frugivore	25	34	21	30	15	14	18	18
Terrestrial frugivore/insectivore	+	3	3	2	+	2	1	1
Arboreal frugivore/insectivore	22	26	23	25	22	34	27	35
Ground insectivore	4	3	5	4	4	3	1	+
Foliage insectivore	9	18	10	23	19	27	23	22
Bark insectivore	14	6	14	4	8	3	1	1
Flycatching insectivore	2	1	1	2	1	2	1	2
Army-ant followers	11	1	8	1	1	+		
Nectarivore/insectivore	11	5	13	8	28	14	25	16
Granivore	1		1		+			
Carnivore	+	1	+	+	+	+		
Piscivore	+							
Epiphyte insectivore			+		1	2	2	5
Nectarivore/frugivore	+	+		+		+		

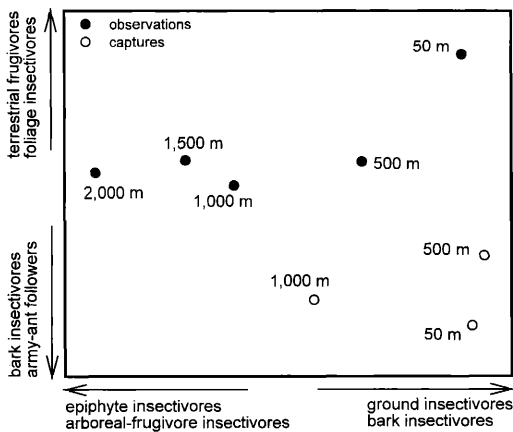


FIG. 8. Nonmetric multidimensional scaling ordination of study locations based on captures or observations of individuals within trophic groups. Distance between points indicates degree of similarity.

nounced when proportions of species per group were compared.

The relative importance of trophic groups varied among forest life zones (Fig. 8). Arboreal frugivores were more important at lower elevations (50 to 500 m), whereas arboreal frugivore/insectivores were more important above 500 m. Similarly, nectarivores were proportionately more important at higher elevations. These and other differences (e.g. greater importance of army-ant followers in capture data than in count data) between netting and count data and among habitats were reflected in the ordination (Fig. 8).

Similarity values based on the proportion of individuals among trophic groups were considerably higher than values based on proportions among species (Tables 2, 4). Thus, turnover in species composition among forests was

TABLE 4. Jaccard similarity indices based on proportion of individuals per trophic group.

	Captures			Observations			
	50 m	500 m	1,000 m	50 m	500 m	1,000 m	1,500 m
Captures							
500 m	0.84						
1,000 m	0.56	0.61					
Observations							
50 m	0.60	0.59	0.56				
500 m	0.62	0.60	0.60	0.81			
1,000 m	0.49	0.53	0.63	0.56	0.67		
1,500 m	0.49	0.53	0.75	0.56	0.66	0.73	
2,000 m	0.48	0.51	0.61	0.54	0.62	0.82	0.78

much greater than turnover in trophic composition of the avifauna. Furthermore, similarity matrices were different (Mantel test, $r = 0.19$, $P > 0.10$), indicating that relative similarities among habitats also differed (Figs. 4 and 8).

DISCUSSION

Data from point counts and mist nets demonstrate the high diversity of species along the transect from La Selva to Volcán Barva in the Cordillera Central of Costa Rica. The importance of this region for conservation is evident from the number of species present, the high variation in species composition from one life zone to another, and the presence of many threatened species, including several (*Spizaetus tyrannus*, *Crax rubra*, *Pharomachrus mocinno*) on the Costa Rican endangered or vulnerable species list (Stiles 1985). Many elevational migrants occur along this gradient, illustrating the importance of protecting forests from lowlands to montane regions. Little forest remains in the Caribbean lowlands of Costa Rica, making this gradient especially important as a refuge for many species. Our results provide strong support for Young et al.'s conclusion regarding the need to protect lower-elevation forests in the Cordillera de Tilarán (see also Powell and Bjork 1994).

Community composition.—Declines in species number with elevation have been reported for many types of organisms (Rosenzweig 1995), although peak species richness often is not found at the lowest elevation. Bird-species diversity changed little from 50 to 1,000 m along the transect from La Selva to Volcán Barva, but netting and count data both suggested that diversity was highest at 500 m (after correcting

for sample size). Despite the similar number of species at these sites, species composition changed substantially, particularly from 500 m to 1,000 m. Species richness was much lower at 1,500 and 2,000 m, with few species shared with sites at 50 and 500 m. These data indicate that turnover in species composition occurs over relatively short distances but also that distance per se is not the sole cause of differences in species composition. The two lowest sites (50 m, 500 m) were the farthest apart (ca. 10 km) but were the most similar in terms of species number and composition.

Changes in community composition from one elevation to the next reflect many factors that affect the distributional patterns of individual species. Such factors may operate over various temporal and spatial scales. For example, some of the turnover in species composition from low to higher forests may reflect relatively recent (past several decades) changes in land use that likely have affected bird populations at La Selva. With increasing deforestation in the Caribbean lowlands, La Selva has gone from being part of a larger area of continuous forest to being the tip of a peninsula of forest. Anecdotal accounts (S. Hilty and D. Wolf pers. comm.) and long-term observations (Levey and Stiles 1994) suggest that populations of a number of species have declined at La Selva during the past few decades. Species such as *Chlorothraupis carmioli*, *Tachyphonus delatrii*, and several antwrens were common on our study plot at 50 m when we began this study but now appear to be less common. These species still are commonly encountered at higher elevations (e.g. 500 m) within Braulio Carrillo National Park. Changes in species composition as a consequence of changing patterns of land use likely

will be an increasingly important aspect of community dynamics and turnover along elevational gradients in Costa Rica and elsewhere.

Many changes in community composition with elevation reflect changes in the types of resources present. Insectivorous species, for example, generally are less important at higher elevations (Terborgh 1971), but the declines vary among groups. Decreased relative importance of large (>100 g) insectivorous species at higher elevations may, for example, be associated with decreased abundance of large insects (Janes 1994). Species that follow army ant (e.g. *Eciton burchelli*) swarms are diverse and common at low (50 and 500 m) elevations along the gradient, less common at 1,000 m, and absent from higher elevations. This trend follows the pattern of ant distribution; army ants were rarely seen at elevations above 500 m (see also Olson 1994). The swarms that we observed at 1,000 m typically were smaller and attended by fewer individual birds and fewer species. In contrast, species that primarily forage in epiphytes are more common at higher elevations, reflecting the greater importance of epiphytic plants at such elevations. Some insectivorous groups that are particularly common and important components of lowland avifaunas are rare or absent at higher elevations, reflecting historical patterns of diversification. For example, all members of the Thamnophilidae, Formicariidae, and Dendrocolaptidae are insectivores, and species diversity within each group is higher at lower elevations in the Neotropics (Parker et al. 1996, Renjifo et al. 1997). Furnariids, by contrast, are more common at higher elevations.

Nectarivores and frugivores are important components of most tropical forests and frequently increase in relative importance with elevation (Terborgh 1971, Stiles 1985). Greater importance of nectarivores at higher elevations parallels changes in the importance of bird-pollinated plants (Stiles 1985), particularly epiphytic species in the Gesneriaceae and Ericaceae (Gentry 1988). A similar pattern helps explain the increased relative importance of frugivores at higher elevations in many tropical forests. As with insectivores, however, many of the larger frugivores are less common at higher elevations.

Temporal and spatial variation in resources exert a major influence on many bird assem-

blages and affect distribution patterns along elevational gradients. Fruit and nectar may be more easily obtained than many insects and typically are less subject to short-term, weather-induced fluctuations in abundance or availability. Seasonal and annual fluctuations in flower and fruit production can be great, however, with phenological patterns differing among elevations. Such phenological variation in an important contributor to the elevational movement patterns of many species (Stiles 1983, Loiselle and Blake 1991, Rosselli 1994). Of the 56 elevational migrants recorded during this study, 60% were frugivores and 25% were nectarivores. Representation of these two groups among migrants is much greater than predicted by their representation in the highland avifauna (Levey and Stiles 1994).

Migrants were an important component of the avifauna along the entire gradient, but the relative importance of latitudinal and elevational migrants differed among elevations. Latitudinal migrants frequently are more common in second-growth habitats (Blake and Loiselle 1992, Petit et al. 1995). Within old-growth forest, however, latitudinal migrants frequently are more common at low to mid-elevations (1,000 m) where many join mixed-species flocks (pers. obs.). Such behavior was less commonly observed in the low-elevation forests (50 and 500 m). Elevational migrants, in contrast, are more common in mature forest than in second growth (Blake et al. 1990). Annual variation in movements of migrants from high to low elevations can be pronounced (Loiselle and Blake 1992) and can be more pronounced in second-growth than in old-growth forests (Blake and Loiselle unpubl. data). As discussed above, most elevational migrants rely on fruit or nectar, and annual variation in movement patterns likely reflects annual variation in flowering and fruiting of preferred plants. Elevational migrants make up a large proportion of the avifauna at higher elevations in Braulio Carrillo, and their occurrence contributes to the dynamic nature of the avifaunas in those forests (Stiles 1985).

Conservation efforts often are focused on regions or sites that support threatened, endemic, or rare species. Thus, knowledge of the distribution patterns of threatened species can be an important argument for protection of different areas (Wege and Long 1995). In our study,

threatened species were equally common from 50 to 1,500 m, illustrating the need to protect forest along the entire transect. Threatened species were less important at 2,000 m, perhaps because of the greater overall protection of higher-elevation forests in Costa Rica. In other regions, montane avifaunas are among the most in need of protection (Renjifo et al. 1997).

Mist nets and point counts.—Mist nets and point counts have been used to sample understory birds in many tropical forests. Use of mist nets continues to be controversial, although much of the controversy is unwarranted. Mist nets do not sample all birds in any habitat, nor do they provide estimates of density and perhaps not of relative abundance (Remsen and Good 1996). However, despite statements to the contrary, few workers have suggested that mist nets could be used to provide a complete enumeration of all species in a forest. Point counts also have many biases and limitations and are especially subject to observer differences, which can be large. Detections of birds by sight and sound are affected by wind, rain, vegetation structure, behavior of birds and observers, and many other factors. Although some of these factors can be controlled (e.g. not counting during rain), others are more difficult to account for (e.g. differences in abilities of observers). As recent publications (Whitman et al. 1997, Rappole et al. 1998) have noted, point counts typically detect more species, but mist nets often are more effective for detecting certain types of birds. No sampling technique is free of biases or effective for all groups, and a combination of techniques is most useful in many cases (Terborgh et al. 1990).

Despite their differences, netting data and count data provided comparable descriptions of many general patterns in the distribution and richness of species along the elevational gradient in the Cordillera Central. For example, nets and counts revealed similar patterns in relative distribution of migrants and threatened species among life zones. Nonetheless, important differences existed in results obtained by the two methods. Of 40 families represented, 10 were only recorded during point counts. Although most of these families were represented by only one or two species, Psittacidae (8 species) and Cotingidae (4 species) are important families numerically and ecologically (i.e. as seed predators and seed dispersers). Many spe-

cies typically found above net level, either in the mid-story (e.g. several trogons) or the canopy (e.g. tanagers and honeycreepers) were rarely, if ever, captured in nets. In contrast, rare or inconspicuous species (e.g. latitudinal migrants that rarely vocalize during the non-breeding season) often were overlooked during counts. Ninety-three species recorded during counts were never captured; 35 species were captured but not recorded during counts. Furthermore, nets and counts differed not only in what species were detected but also in how frequently different species were detected.

Mist nets typically do not catch large birds, so those species were under-represented (or absent) in our capture data. Such species, which include tinamous, cracids, and parrots, are important components of tropical avifaunas in terms of biomass and their roles as seed dispersers and seed predators (Karr et al. 1990, Terborgh et al. 1990). Both sampling methods indicated a decline in large species with elevation, something that has been noted previously (Beehler 1981, Janes 1994), but estimates of the proportional occurrence of large birds at different elevations differed between the two data sets. Netting and count data also differed in relative importance of some trophic groups; nectarivores, ground insectivores, and ant-following insectivores were more common in netting data, whereas foliage insectivores and arboreal frugivores were more important in count data.

Tropical forest avifaunas typically are characterized by the presence of many rare species (Karr et al. 1990, Terborgh et al. 1990), and species-accumulation curves typically indicate that new species are continually added to mist-net samples as numbers of captures increase. New species reflect both the occasional capture of relatively common birds that typically occur above mist-net level as well as species rarely encountered in the habitat. Accumulation curves indicated that netting samples in our study had not reached a plateau at any elevation; species still were being added at a regular rate even after 4,000 captures in lowland wet forest (50 m). In contrast, accumulation curves based on count data tended to approach an asymptote for most sites, suggesting that most of the common species had been detected. Additional species are known from all these sites, however, so additional counts, particularly in

different seasons, clearly would add more species to the total.

Cordillera Central and Cordillera de Tilarán.—Costa Rica is characterized by a series of mountain ranges, or cordilleras, that run from the border with Panama (Cordillera de Talamanca) to the northwestern part of the country (Cordillera de Guanacaste). The two central cordilleras, Cordillera Central and Cordillera de Tilarán, have been the sites of several studies of birds along elevational gradients. Both regions are biologically diverse and are important areas for conservation, but they differ in a variety of features that can influence patterns of bird distribution. The Cordillera Central reaches more than 2,900 m along the La Selva/Volcán Barva transect, whereas the Cordillera de Tilarán reaches a maximum of about 1,860 m in the Monteverde region (ca. 80 to 85 km to the northwest). The Cordillera Central also covers a much greater area than does the Cordillera de Tilarán. Finally, mature forest is protected along the entire elevational gradient in the Cordillera Central but not on the Caribbean slope of the Monteverde region.

Young et al. (1998) summarized data from netting studies conducted in five forest life zones in the Monteverde region of the Cordillera de Tilarán: wet premontane, transition (650 to 750 m on Caribbean slope); lower montane wet (1,400 to 1,550 m on Pacific slope); premontane wet (1,000 to 1,400 m on Pacific slope); lower montane rain (1,500 to 1,700 m on continental divide); and premontane rain (750 to 1,450 m on Caribbean slope). We have netting data from two of these zones (tropical wet, cool transition forest [500 m], which is similar to wet premontane transition; and premontane rain forest [1,000 m]) and count data from a third (lower montane rain forest [1,500 and 2,000 m]); all of our data are from the Caribbean slope.

Both Young et al. and our study documented high species diversity and high turnover along the elevational gradients. Young et al. reported 235 species from 10,726 captures compared with our 168 species in 7,312 captures. Species totals were higher for all zones in the Monteverde region, either in comparison with our netting totals or our count totals. Much of the difference can be attributed to their inclusion of data from second-growth habitats given that all of our data were from mature forests. Inclusion

of second-growth habitats at La Selva would have brought our total number of species recorded to 343, including 249 species captured in nets and 301 species observed in counts (Blake and Loiselle unpubl. data). The presence of Pacific slope birds in the Monteverde data set, species not present on the Caribbean slopes of Braulio Carrillo, also contributed to the observed differences in species numbers between study sites in the Cordillera de Tilarán and the Cordillera Central.

Patterns in community composition were similar in many respects between the two areas. The four most species-rich families in both studies were tyrannids, trochilids, parulids, and thraupids. Similarly, elevational patterns for many families were the same (e.g. dendrocolaptids and thamnophilids were more common at lower elevations; rhinocryptids and ptilogonatids were restricted to high elevations). The number of species captured per family was highly correlated between the two data sets ($r = 0.94$, $P < 0.001$). Despite these similarities, important differences existed between the two data sets. We recorded species from several important families that were not represented in the netting data of Young et al. (e.g. Tinamidae, Accipitridae, Cracidae, Cotingidae); most of these species were documented during counts, and most are known from the Monteverde area as well (Fogden 1993). Furthermore, many columbids, psittacids, trogonids, ramphastids, and tyrannids were not captured in nets but were common in counts; many of these species were not present in the Monteverde data set. Other differences were not, however, related to sampling methods. Young et al. found 15 species across the entire range of life zones, but we recorded only two species (*Mionectes olivaceus*, *Myadestes melanops*), both elevational migrants, from the lowest to the highest elevations. Such regional differences likely reflect the abruptness of life zones, the inclusion of second-growth habitats in all zones in the Monteverde study (many second-growth birds have wide elevational ranges), and the narrower range of elevations covered in Monteverde (650 to 1,700 m vs. 50 to 2,000 m in our study).

Both studies documented high turnover in species composition from one life zone to another over relatively short distances. Beta diversity for the Monteverde data set was 0.45, whereas beta diversity in our study was 0.60

based on netting data from three elevations and 0.52 based on count data from five elevations. Jaccard similarity values ranged from 0.19 to 0.47 in Monteverde and from 0.20 to 0.56 (netting) and from 0.01 to 0.62 (counts) in our study. Thus, both mountain ranges illustrate the importance of species turnover along elevational gradients as a factor influencing the species richness of the regions. High faunal turnover along elevational gradients is characteristic of other groups as well (e.g. trees, Lieberman et al. 1996; leaf-litter invertebrates, Olson 1994).

Avifaunas of both regions of Costa Rica are characterized by a high proportion of elevational migrants, although totals are somewhat higher along the La Selva/Volcán Barva transect. The occurrence of many elevational migrants at low elevations emphasizes the value of protecting forest along an entire gradient. Such protection does not exist in the Monteverde area but is warranted not only because many species regularly move to lower elevations, but also because other species may move to lower elevations only on an irregular basis (*Pipra pipra* occasionally moves from higher elevations in Braulio Carrillo to second growth at La Selva). Although such movements may occur only infrequently, they involve many individuals in some years (Winker et al. 1997). The presence of lowland refugia during periods of inclement weather or low resource conditions at higher elevations may ensure long-term survival of species.

The lowest elevation represented in the data of Young et al. was 650 m. Absence of lowland wet forest sites from the Caribbean slope likely reduced the total number of species captured. In our study, 117 species were not recorded above 500 m, and 27 species were found only at 50 m. Of the 117 species, 71 were not recorded by Young et al., although many of these species are known from the Monteverde area, particularly from the lower regions of the Caribbean slope (Fogden 1993). We captured 39 of the 71 species, suggesting that the absence of many of these species from the Monteverde data set was not simply due to lack of counts. These data further illustrate the need to protect lower-elevation forests in the Tilarán region if long-term survival of many species is to be assured.

Substantial variation in the structure and composition of forest avifaunas occurs in the

mountains of Costa Rica. Turnover and diversity patterns are similar between two well-studied cordilleras, likely indicating similar evolutionary histories and historical development of their respective avifaunas. Both studies highlight the distinctiveness of avifaunas among Holdridge life zones and the relatively high proportion of threatened species and species that undergo regular seasonal movements from one zone to another. Thus, the integrity of biodiversity in Costa Rica requires not only the preservation of representatives of each life zone, but also connections among such zones.

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APPENDIX 1. Continued.

Species ^a	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
Bronzy Hermit (<i>Glaucis aenea</i>)	0.02		0.06							
Band-tailed Barthroath (<i>Threptes ruckeri</i>)	0.30		0.17							
Green Hermit (<i>Phaethornis guy</i>) E			2.83	0.27	10.83	4.08	8.20	2.13		
Long-tailed Hermit (<i>Phaethornis superciliosus</i>)	5.68	1.68	2.08	1.47						
Little Hermit (<i>Phaethornis longuemareus</i>)	0.50	1.09	0.63	1.10	0.45					
White-tipped Sicklebill (<i>Eutoxeres aquila</i>) E	0.17	0.08	0.35		0.84		0.10			
Green-fronted Lancebill (<i>Doryfera ludovicianae</i>) E			0.06		0.97	0.09				
Violet Sabrewing (<i>Campylopterus hemileucurus</i>) E					0.06					
White-necked Jacobin (<i>Florisuga mellivora</i>) E	0.69	0.03	0.81	0.09					0.11	
Green Violet-ear (<i>Colibri thalassinus</i>)										
Violet-headed Hummingbird (<i>Klais guineii</i>)	0.07		0.23	0.73						
Canivet's Emerald (<i>Chlorostilbon canivetii</i>)			0.06							
Violet-crowned Woodnymph (<i>Thalurania colombica</i>) E	1.66	0.68	3.46	1.74	1.35	0.19	0.14	6.67		
Fiery-throated Hummingbird (<i>Penterte insignis</i>) E										
Blue-throated Goldentail (<i>Hylocharis eliciae</i>) E	0.05		0.06							
Blue-chested Hummingbird (<i>Amazilia amabilis</i>)	0.07									
Rufous-tailed Hummingbird (<i>Amazilia tzacatl</i>)										
Black-bellied Hummingbird (<i>Eupherusa nigricentris</i>) E,T					2.90	1.57	7.25			
Coppery-headed Emerald (<i>Eivira cupreiceps</i>) E,T			0.06		0.45	0.09				
Snowcap (<i>Microchera Albocoronata</i>) E,T	1.54	0.14	2.42	0.09						
Bronze-tailed Plumeteer (<i>Chalybura urochrysia</i>) T					5.48	3.10				
White-bellied Mountain-gem (<i>Lampornis hemileucus</i>)					0.06		5.77	2.68		
White-throated Mountain-gem (<i>Lampornis castaneiventris</i>) E					4.84	0.28	0.52	0.27		
Green-crowned Brilliant (<i>Heliodoxa jacula</i>) E										
Purple-crowned Fairy (<i>Heliothryx barroti</i>)	0.02	0.01								
Long-billed Starthroat (<i>Helioaster longirostris</i>)										
Scintillant Hummingbird (<i>Selasphorus scintilla</i>) E										
Collared Trogon (<i>Trogon collaris</i>) E					0.13	1.02	0.05	0.22		
Orange-bellied Trogon (<i>Trogon aurantiiventris</i>)					0.13		0.91	0.11		
Black-throated Trogon (<i>Trogon rufus</i>)	0.40	2.36	0.12	1.83						
Slaty-tailed Trogon (<i>Trogon massena</i>)	1.79	0.72	1.24	1.01						
Lattice-tailed Trogon (<i>Trogon clathratus</i>) E										
Resplendent Quetzal (<i>Pharomacrus mocino</i>) E,T										
Rufous Motmot (<i>Baryphthengus martii</i>)	0.27	0.19	0.12	1.33	0.06					
Broad-billed Motmot (<i>Electron platyrynchum</i>)	0.17	0.73								
American Pygmy Kingfisher (<i>Chloroceryle aenea</i>)	0.02									
White-necked Puffbird (<i>Notharchus macrorhynchos</i>)		0.01								
White-whiskered Puffbird (<i>Malacoptila panamensis</i>)	0.15		0.17							

APPENDIX 1. Continued.

Species ^a	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
White-fronted Numbird (<i>Monasa morphoeus</i>)	0.02	0.81		1.65						
Great Jacamar (<i>Jacamerops aurea</i>)		0.15								
Red-headed Barbet (<i>Eubucco bourcierii</i>) E					0.06	0.14				
Prong-billed Barbet (<i>Semnornis frantzii</i>) E					0.64	4.17		6.49		3.55
Emerald Toucanet (<i>Aulacorhynchus prasinus</i>) E					0.06	0.28		0.24		0.27
Collared Aracari (<i>Pteroglossus torquatus</i>)	0.40	1.87		1.60						
Yellow-eared Toucanet (<i>Selenidera spectabilis</i>) E, I		0.12								
Keel-billed Toucan (<i>Ramphastos sulfuratus</i>)		2.45		1.42						
Chestnut-mandibled Toucan (<i>Ramphastos swainsonii</i>) T		2.83		1.28						
Black-cheeked Woodpecker (<i>Melanerpes pucherani</i>)		0.10		0.18						
Hairy Woodpecker (<i>Picoides villosus</i>)						0.05		0.05		0.66
Rufous-winged Woodpecker (<i>Piculus simplex</i>) T		0.03		0.09						
Golden-olive Woodpecker (<i>Piculus rubiginosus</i>)		0.06				0.28		0.48		
Cinnamon Woodpecker (<i>Celexus lorricatus</i>)		0.40		0.14						
Chestnut-colored Woodpecker (<i>Celexus castaneus</i>)		0.16		0.09						
Linedated Woodpecker (<i>Dryocopus lineatus</i>)		2.42		1.37						
Pale-billed Woodpecker (<i>Campephilus guatemalensis</i>)	0.02									
Spotted Barbtail (<i>Premnoplex brunescens</i>)					3.80	0.93		0.86		0.60
Ruddy Treerunner (<i>Margarornis rubiginosus</i>)								0.81		3.66
Buffy Tuftedcheek (<i>Pseudocolaptes lawrencii</i>)								0.05		0.27
Striped Woodhaunter (<i>Hylocistis subulatus</i>)										
Linedated Foliage-gleaner (<i>Syndactyla subalaris</i>)	0.22	0.11		0.63						
Scaly-throated Foliage-gleaner (<i>Anabacerthia variegaticeps</i>) T										
Buff-throated Foliage-gleaner (<i>Automolus ochrolaemus</i>)	0.05	0.02		0.92				0.29		0.22
Streak-breasted Treehunter (<i>Thripadectes rufobrunneus</i>) T					0.06					
Plain Xenops (<i>Xenops minutus</i>)	0.45	0.06		0.52						
Tawny-throated Leaf-tosser (<i>Sclerurus mexicanus</i>)				0.12						
Scaly-throated Leaf-tosser (<i>Sclerurus guatemalensis</i>) T				0.23						
Plain-brown Woodcreeper (<i>Dendrocincla fuliginosa</i>)	0.92	0.03		0.52						
Ruddy Woodcreeper (<i>Dendrocincla homochroa</i>)	1.46	0.02		0.05						
Long-tailed Woodcreeper (<i>Deconychura longicauda</i>)	0.02	0.01		0.05						
Wedge-billed Woodcreeper (<i>Glyphorhynchus spirurus</i>)	12.56	1.83		12.98						
Northern Barred Woodcreeper (<i>Dendrocolaptes sanctithomae</i>)	0.47	0.32		0.09						
Cocoa Woodcreeper (<i>Xiphorhynchus susurrans</i>)	0.05									
Black-striped Woodcreeper (<i>Xiphorhynchus lachrymosus</i>)	0.12	1.11		0.73						
Spotted Woodcreeper (<i>Xiphorhynchus erythropygius</i>)	0.72	0.14		0.05						
Brown-billed Scythebill (<i>Campylorhamphus pusillus</i>) E				0.98						1.30
Fasciated Antshrike (<i>Cymbilaimus lineatus</i>)				0.29						0.19
				0.14						

APPENDIX 1. Continued.

Species ^a	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
Great Antshrike (<i>Taraba major</i>)				0.05						
Western Slaty-Antshrike (<i>Thamnophilus atrinucha</i>)	0.52	0.66								
Russet Antshrike (<i>Thamnistes anabatinus</i>)			0.06							
Plain Antvireo (<i>Dysithamnus mentalis</i>) E					2.06	0.23				
Streak-crowned Antvireo (<i>Dysithamnus striaticeps</i>) T	0.32	0.09	0.87	0.18						
Checker-throated Antwren (<i>Myrmotherula fulviventris</i>)	0.84	0.02	0.29	0.09						
White-flanked Antwren (<i>Myrmotherula axillaris</i>)	0.45	0.14	0.46	0.50						
Slaty Antwren (<i>Myrmotherula schisticolor</i>)					1.61	0.23				
Dot-winged Antwren (<i>Microhopias quixensis</i>)				0.09						
Chestnut-backed Antbird (<i>Myrmeciza exsul</i>)	0.62	2.20	1.04	2.15						
Immaculate Antbird (<i>Myrmeciza immaculata</i>) E					1.23	1.81		1.86		
Spotted Antbird (<i>Hylophylax naevioides</i>)	1.51	0.20	2.42	0.37						
Bicolored Antbird (<i>Gymnophrys leucaspis</i>)	4.54	0.34	3.17	0.32						
Ocellated Antbird (<i>Phaenostictus mcleannani</i>)	2.78	0.57	1.90	0.37	0.77	0.05				
Black-faced Antthrush (<i>Formicarius analis</i>)	0.87	1.86	0.35	2.25						
Scaled Antpitta (<i>Grallaria guatemalensis</i>) T					0.06					
Streak-chested Antpitta (<i>Hyllopezus perspicillatus</i>)	0.05	0.44	0.29	0.55					0.16	
Ochre-breasted Antpitta (<i>Grallaricula flavirostris</i>)					0.39	0.09			2.69	4.81
Silvery-fronted Tapaculo (<i>Scytalophus argentifrons</i>)										
Brown-capped Tyrannulet (<i>Ornithion brunneicapillum</i>)	0.02	0.01								
Mountain Elaenia (<i>Elaenia frantzii</i>) E									0.19	1.75
Olive-striped Flycatcher (<i>Mionectes olivaceus</i>) E	1.49	0.01	1.21		7.80	0.19			0.72	0.05
Ochre-bellied Flycatcher (<i>Mionectes oleagineus</i>) E*	9.23	0.23	7.27	0.41	0.06					
Slaty-capped Flycatcher (<i>Leptopogon superciliosus</i>)			0.06							
Paltry Tyrannulet (<i>Zimmerius villosus</i>) E	0.02	0.85		1.05	0.06	1.95		1.81		
Black-capped Pygmy-Tyrant (<i>Myiornis atricapillus</i>)	0.02	0.62		0.14					2.59	0.52
Scale-crested Flycatcher (<i>Lophotriccus pileatus</i>)			0.12	0.14	1.03	2.59				
Eye-ringed Flatbill (<i>Rhynchocyclus brevirostris</i>)	0.52	0.30	0.06	0.23	0.13					
Yellow-margined Flycatcher (<i>Tolmomyias assimilis</i>)	0.07	0.35								
White-throated Spadebill (<i>Platyrinchus mystaceus</i>)	0.74	0.30	1.96	0.18	2.13	0.23		0.57	0.27	
Golden-crowned Spadebill (<i>Platyrinchus coronatus</i>)	0.20		0.12							
Royal Flycatcher (<i>Onychorhynchus coronatus</i>)	1.69	0.09	0.46							
Ruddy-tailed Flycatcher (<i>Terenotriccus erythrurus</i>)			0.17							
Sulphur-rumped Flycatcher (<i>Myiobius sulphureipygius</i>)					0.13	1.34		1.10		
Tufted Flycatcher (<i>Mitrophanes phaeocercus</i>)					0.13	0.05				
Olive-sided Flycatcher (<i>Contopus cooperi</i>) L	0.05	0.05								
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>) L	0.30	0.05	0.06							
Acadian Flycatcher (<i>Empidonax vireescens</i>) L					0.19					

APPENDIX 1. Continued.

Species*	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
White-throated Flycatcher (<i>Empidonax albigularis</i>)										0.82
Yellowish Flycatcher (<i>Empidonax flavescens</i>) E					0.58	0.37	0.14		0.71	
Black-capped Flycatcher (<i>Flavescens atriceps</i>) E										0.16
Bright-rumped Atiila (<i>Atiila spadiceus</i>)	0.27	1.89	0.12	2.02	0.13	0.46	0.52			
Rufous Mourner (<i>Rhytipterna holerythra</i>)	0.10	1.00	0.06	1.28	0.06	0.32				
Great Crested Flycatcher (<i>Myiarchus crinitus</i>) L		0.33								
Boat-billed Flycatcher (<i>Megarynchus pitangua</i>)		0.05								
Gray-capped Flycatcher (<i>Myizetetes granadensis</i>)		0.08		0.09						
Golden-bellied Flycatcher (<i>Myiodynastes hemichrysus</i>)									0.56	0.11
Thrush-like Shiffornis (<i>Schiffornis turdinus</i>)			0.29						0.42	
Gray-headed Piprites (<i>Piprites griseiceps</i>) T	0.02	0.05	0.06	0.50						
Rufous Pika (<i>Lipaugus unirufus</i>)	0.02	2.15	0.06	3.67						
Masked Tityra (<i>Tityra semifasciata</i>)	0.05	0.28		0.05						
Snowy Cotinga (<i>Carpodectes nitidus</i>) T		0.01								
Purple-throated Fruitcrow (<i>Querula purpurata</i>)		0.76		0.09						
Bare-necked Umbrellabird (<i>Cephalopterus glabricollis</i>) E,T		0.06					0.28			
Three-wattled Bellbird (<i>Procnias tricarunculata</i>) E,T		0.20		1.19			1.85		0.86	
White-collared Manakin (<i>Manacus candei</i>)	0.52		0.06							
White-throated Manakin (<i>Corapipo altera</i>) E	6.23	0.10	14.60	0.23	0.32					
White-crowned Manakin (<i>Pipra pipra</i>) E	0.07		0.23		4.06		0.19			
Red-capped Manakin (<i>Pipra mentalis</i>) E*	16.41	1.42	4.33	1.92						
Sharpbill (<i>Oxyruncus cristatus</i>) E							0.05			0.60
Yellow-winged Vireo (<i>Vireo carmioti</i>) E		0.02								
Philadelphia Vireo (<i>Vireo philadelphicus</i>) L		0.02								
Red-eyed Vireo (<i>Vireo olivaceus</i>) L		0.73		0.87						
Tawny-crowned Greenlet (<i>Hylophilus ochraceiceps</i>)	0.74	0.02	0.87	0.87						
Lesser Greenlet (<i>Hylophilus decurtatus</i>)	0.02	2.68	0.06	2.70			0.19			
Green Shrike-Vireo (<i>Vireolanium pulchellus</i>)		0.07		2.15						
Azure-hooded Jay (<i>Cyanolyca cucullata</i>)					0.13		0.46		0.91	
Bay Wren (<i>Thryothorus nigricapillus</i>)	0.05	0.39	0.06	0.27						
Stripe-breasted Wren (<i>Thryothorus thoracicus</i>)	0.02	0.08	0.06	2.29						
Ochraceous Wren (<i>Troglodytes ochraceus</i>)										
White-breasted Wood-Wren (<i>Henicorhina leucosticta</i>)	2.48	3.64	1.33	3.80						
Gray-breasted Wood-Wren (<i>Henicorhina leucosticta</i>)										
Nightingale Wren (<i>Microcerculus philomela</i>) T	0.72	0.57	0.17	0.41						
Song Wren (<i>Cyphorhinus phaeocephalus</i>)	0.92	0.24	3.29	1.19						
Tawny-faced Gnatwren (<i>Microbatas cinereiventris</i>)	0.67	0.01	0.63	0.41	0.19		0.23			
Long-billed Gnatwren (<i>Ramphocaelus melanurus</i>)		0.02	0.06	0.55			0.05			

APPENDIX 1. Continued.

Species ^a	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
Tropical Gnatcatcher (<i>Poliophtila plumbea</i>)		1.06								
Black-faced Solitaire (<i>Myadestes melanops</i>) E	0.32		0.58	0.78	6.58	3.06	9.11		6.34	
Black-billed Nighthale-Thrush (<i>Catharus gracilirostris</i>)					2.90	1.44	1.76		3.66	
Slaty-backed Nighthale-Thrush (<i>Catharus fuscescens</i>)										0.93
Ruddy-capped Nighthale-Thrush (<i>Catharus frontzii</i>)										
Black-headed Nighthale-Thrush (<i>Catharus mexicanus</i>)										
Gray-cheeked Thrush (<i>Catharus minimus</i>) L			0.17							
Swainson's Thrush (<i>Catharus ustulatus</i>) L	0.07		0.12		1.10					
Wood Thrush (<i>Hylocichla ustelina</i>) L,T	0.94		1.21	0.05	0.19					
Mountain Robin (<i>Turdus plebejus</i>) E	5.26	0.56	3.35	1.19	0.19					
Pale-vented Robin (<i>Turdus obsoletus</i>) E	0.77		1.50	0.09	3.93	2.13	0.19		3.11	
Black-and-yellow Silky-flycatcher (<i>Phainoptila melanoxantha</i>)										
Long-tailed Silky-flycatcher (<i>Ptilogenys caudatus</i>) E					0.06	0.09			2.84	
Golden-winged Warbler (<i>Vermivora chrysoptera</i>) L,T						0.19			0.33	
Chesnut-sided Warbler (<i>Dendroica pensylvanica</i>) L	0.02	1.07	0.06	1.10		0.14				
Black-throated Green Warbler (<i>Dendroica virens</i>)						0.14				
Blackburnian Warbler (<i>Dendroica fusca</i>) L						0.14				
Bay-breasted Warbler (<i>Dendroica castanea</i>) L	0.02	0.01			0.06	0.05				
Black-and-white Warbler (<i>Mniotilta varia</i>) L	0.02	0.01								
Worm-eating Warbler (<i>Helminthos vermicivorus</i>) L,T	0.02				0.06	0.06				
Ovenbird (<i>Seiurus aurocapillus</i>) L					0.06					
Louisiana Waterthrush (<i>Seiurus motacilla</i>) L	0.07				0.06					
Kentucky Warbler (<i>Oporornis formosus</i>) L	0.17				0.13					
Olive-crowned Yellowthroat (<i>Geothlypis semiflava</i>)	0.02		0.46							
Wilson's Warbler (<i>Wilsonia pusilla</i>) L									0.22	
Canada Warbler (<i>Wilsonia canadensis</i>) L	0.02				0.06					
Slate-throated Redstart (<i>Myioborus miniatus</i>)					2.00	3.01	2.15		3.55	
Collared Redstart (<i>Myioborus torquatus</i>) E									1.04	
Black-cheeked Warbler (<i>Basilentulus melanogenys</i>)					2.26	0.51	1.62			
Three-striped Warbler (<i>Basilentulus tristriatus</i>)					0.06	0.14	0.05			
Buff-rumped Warbler (<i>Phaeothlypis fulvicauda</i>)	0.05	0.01	0.23							
Wrenthrush (<i>Zeledonia coronata</i>)										0.11
Bananaquit (<i>Coereba flaveola</i>)					0.13	2.41	16.12			
Common Bush-Tanager (<i>Chlorospingus ophthalmicus</i>)		0.05			3.22	17.74	0.05		0.05	
Sooty-capped Bush-Tanager (<i>Chlorospingus pileatus</i>)										26.07
Black-and-yellow Tanager (<i>Chrysothlypis chrysomelaena</i>) T										
Dusky-faced Tanager (<i>Mitrospingus cassinii</i>)					0.19	0.97				
Olive Tanager (<i>Chlorothraupis carmioli</i>)	1.94	0.53	0.06	2.06	0.26					

APPENDIX 1. Continued.

Species ^a	50 m		500 m		1,000 m		1,500 m		2,000 m	
	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs	Cap	Obs
White-shouldered Tanager (<i>Tachyphonus luctuosus</i>)	0.07	0.19		0.82						
Tawny-crested Tanager (<i>Tachyphonus delatrii</i>)	0.82	0.22	1.44	1.10	0.58	0.74				
Hepatic Tanager (<i>Piranga flava</i>) E						1.16				
Summer Tanager (<i>Piranga rubra</i>) L	0.02	0.01	0.06		0.06					
Passerini's Tanager (<i>Ramphocelus passerinii</i>)	0.05									
Blue-and-gold Tanager (<i>Bangsia arcact</i>) T				0.09	0.06	0.51				
Yellow-crowned Euphonia (<i>Euphonia luteicapilla</i>)	1.02	0.32	0.06	3.16						
Olive-backed Euphonia (<i>Euphonia gouldi</i>)		0.35		0.64						
White-vented Euphonia (<i>Euphonia minuta</i>)			0.75	0.05	3.80	1.48	0.24	0.10	0.38	
Tawny-capped Euphonia (<i>Euphonia anneae</i>) E,T										
Golden-browed Chlorophonia (<i>Chlorophonia callophrys</i>) E				0.05						
Emerald Tanager (<i>Tangara florida</i>)		0.03		1.01	0.58	4.08				
Silver-throated Tanager (<i>Tangara icterocephala</i>) E		0.18								
Golden-hooded Tanager (<i>Tangara larvata</i>) E										
Spangle-cheeked Tanager (<i>Tangara dowii</i>) E					0.45	0.83	2.00		1.37	
Blue Dacnis (<i>Dacnis cayana</i>) E	0.07	0.19								
Green Honeycreeper (<i>Chlorophanes spiza</i>)	0.02	0.05		0.05						
Shining Honeycreeper (<i>Cyanerpes lucidus</i>)	0.02	0.41		0.09						
Variable Seedeater (<i>Sporophila americana</i>)	0.35		0.52		0.13					
Thick-billed Seed-Finch (<i>Oryzoborus furnereus</i>)	0.37		0.12		0.06					
Yellow-faced Grassquit (<i>Tiaris olivacea</i>)			0.06							
Slaty Flowerpiercer (<i>Diglossa plumbea</i>)							1.29		1.37	
Sooty-faced Finch (<i>Lysurus crassirostris</i>)					0.45	1.48	0.33		1.09	
Yellow-thighed Finch (<i>Pselliophorus tibialis</i>) E									0.11	
Large-footed Finch (<i>Pezotetes capitalis</i>)										
Chestnut-capped Brush-Finch (<i>Buarremon brunneinuchus</i>)			0.06	1.01	2.64	0.93	0.52			
Orange-billed Sparrow (<i>Arremon aurantirostris</i>)	0.15	0.03	2.83							
Black-striped Sparrow (<i>Arremonops contrirostris</i>)	0.07		0.06							
Slate-colored Grosbeak (<i>Saltator grossus</i>)		0.75		2.75		0.23				
Black-faced Grosbeak (<i>Caryothraustes polioaster</i>)				0.69						
Black-thighed Grosbeak (<i>Pheucticus tibialis</i>) E	0.35	0.05	0.75	0.69	0.19	1.11	1.48	0.27		
Blue-black Grosbeak (<i>Cyanocompsa cyanoides</i>)	0.05	4.15		1.60						
Scarlet-rumped Caticue (<i>Caticus uropygialis</i>)		1.07		1.05						
Chestnut-headed Oropendola (<i>Psarocolius wagleri</i>)		3.70		1.92						
Montezuma Oropendola (<i>Psarocolius montezuma</i>)										

^aT = threatened species; L = latitudinal migrant; E = elevational migrant; E* = counted as elevational migrant above 50 m.

APPENDIX 2. Number of species by family for captures (Cap) and observations (Obs) by elevation (see Table 1) in the Cordillera Central, Costa Rica.

Family	50 m		500 m		1,000 m		1,500 m	2,000 m	Species			Zones per species	
	Cap	Obs	Cap	Obs	Cap	Obs	Obs	Obs	Tot	Cap	Obs	Cap	Obs
Tinamidae	1	2	1	2	1	2	1	1	3	2	3	1.0	2.0
Accipitridae	1	2	1	2	1	3			4	2	3	1.5	2.0
Falconidae	2	3		1	1	2			3	2	3	2.0	2.3
Cracidae	2	2		2		1	1	1	3	2	3	1.0	2.7
Odontophoridae		1					1		2		2		1.5
Rallidae		1	4			2			1		1		1.0
Columbidae	3	4		2		3	2	1	8	4	7	1.8	1.6
Psittacidae		6		4		1		1	8		8		1.8
Cuculidae		2		1					2		2		2.0
Strigidae		2		1					2		2		1.5
Caprimulgidae			14	1		9			1		1		1.0
Trochilidae	12	7	1	7	11	3	7	6	27	23	19	1.6	1.9
Trogonidae	1	3	1	3	2		2	2	6	3	5	2.0	2.6
Momotidae	2	2		1	1				2	2	2	2.0	1.5
Alcedinidae	1		1						1	1		1.0	
Bucconidae	2	2		1					3	2	2	1.5	1.5
Galbulidae		1				3			1		1		1.0
Ramphastidae	1	4		3	3	2	2	2	7	4	7	1.0	2.0
Picidae	1	6	5	5		4	2	1	8	1	8	1.0	2.0
Furnariidae	4	4	4	2	5	2	5	5	11	9	10	1.6	2.0
Dendrocolaptidae	7	6		6	4				9	9	7	1.7	2.0
Thamnophilidae	8	8	8	10	4	4	1	1	15	11	14	1.8	1.6
Formicariidae	2	2	2	2	2	1		1	4	4	3	1.5	2.0
Rhinocryptidae						1	1	6	1		1		3.0
Tyrannidae	14	16	12	9	13	10	10		28	20	25	2.0	2.0
<i>Incertae sedis</i>	3	3	3	3		1			4	4	4	1.5	1.8
Cotingidae		4		2		2	1		4		4		2.3
Pipridae	4	2	4	2	2	1			4	4	3	2.5	1.7
Oxyruncidae						1		1	1		1		1.0
Vireonidae	2	5	2	3		1			6	2	6	2.0	1.7
Corvidae					1	1	1	2	1	1	1	1.0	2.0
Troglodytidae	5	5	5	5	1	2	2		7	6	7	1.8	2.3
Sylviidae	1	3	2	3	1	2		4	3	2	3	2.0	2.7
Turdidae	5	1	6	3	5	3	4	2	10	7	8	2.3	1.9
Ptilonotidae					10		1	4	2		2		1.5
Parulidae	8	4	3	1	1	8	3		19	14	13	1.5	1.5
Coerebidae		1			9	1			1	1	1	1.0	2.0
Thraupidae	9	12	6	11	4	10	4	4	23	16	21	1.5	2.0
Emberizidae	4	1	5	1	1	2	3	3	10	7	6	1.9	1.7
Cardinalidae	1	2	2	3		3	1	1	4	2	4	2.0	2.5
Icteridae	1	3		3					3	1	3	1.0	1.0