BIRD COMMUNITIES IN ANDEAN PREMONTANE FORESTS OF NORTHWESTERN ARGENTINA

Lucio R. Malizia^{1,2}, Pedro G. Blendinger^{2,3}, M. Eva Alvarez², Luis O. Rivera⁴, Natalia Politi⁴, & Guillermo Nicolossi⁵

¹International Center for Tropical Ecology, Department of Biology, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121, USA.

²Laboratorio de Investigaciones Ecológicas de las Yungas, Universidad Nacional de Tucumán, C.C. 34, (4107) Yerba Buena, Tucumán, Argentina.

³E-mail: blendinger@birdecology.com.ar

⁴Centro de Zoología Aplicada, Universidad Nacional de Córdoba, C.C. 122, (5000) Córdoba, Argentina.

⁵Parque Nacional Calilegua, Administración de Parques Nacionales, San Lorenzo s/n, (4514) Calilegua, Jujuy, Argentina.

Resumen. - Comunidades de aves en selvas pedemontanas andinas del noroeste de Argentina. - Los estudios de aves andinas a la mesoescala (1000's km²) son escasos, pero podrían ser importantes para planificar estrategias de uso y conservación. Aquí describimos la riqueza, composición y abundancia de comunidades de aves de selvas pedemontanas del noroeste de Argentina (c. 2000 km²). Analizamos cambios estacionales entre el período reproductivo y no-reproductivo, poniendo énfasis en migrantes y gremios tróficos. Además, evaluamos diferencias en la avifauna de áreas planas y de ladera. Muestreamos 12 comunidades de aves mediante conteos por puntos, transectas y redes de niebla. Las comunidades de aves cambiaron espacialmente sin relación con la topografía (i.e., áreas planas o de ladera), y no registramos ningún grupo de aves que caracterice estos sitios. La composición de especies varió marcadamente entre estaciones, con más especies durante la estación reproductiva, aunque la abundancia de aves fue similar entre estaciones. Los ensambles de la época reproductiva estuvieron caracterizados por migrantes latitudinales, y los de la época no-reproductiva por migrantes altitudinales. Los gremios de aves insectívoras y de aves granívoras que forrajean en o encima del dosel caracterizaron la estación reproductiva, mientras que los gremios frugívoro-insectívoro e insectívoro que forrajean en todos los estratos del bosque caracterizaron la estación no-reproductiva. De un total de 112 especies registradas, al menos 10 son de interés para su conservación en Argentina, 14 son poco comunes en el Neotrópico y 31 son migrantes, señalando la importancia de la selva pedemontana para la conservación de aves. Gran parte (c. 75%) de la selva pedemontana ha desaparecido o está seriamente degradada. Esta situación debería llevarnos a unir fuerzas entre gobierno, propietarios, ONGs e instituciones académicas para cambiar las políticas de uso y conservación de los recursos naturales de la región.

Abstract. – Studies of Andean avifaunas at the mesoscale (1000's km²) are scarce, but they may prove critical for understanding community structure and for conservation planning. We studied species diversity, composition and abundance of bird communities in premontane forests of northwestern Argentina (c. 2000 km²). We measured changes between breeding and non-breeding seasons, focusing on migrants and trophic guilds, and we compared flat and foothill areas. Twelve bird communities were sampled using point counts, mist nets, and line transects. More species were recorded during the breeding than the non-breeding season, in part due to the arrival of migrants, but the abundance of birds did not differ between

seasons. We registered more individuals and species of migratory birds during the breeding season. Latitudinal and elevational migrants characterized breeding and non-breeding assemblages, respectively. We found no significant differences in bird species richness, composition or abundance in relation to forest type (i.e., flat vs foothill), in part due to the patchy distributions of birds across the entire study area. Different feeding guilds characterized each season: insectivorous and granivorous species that foraged in or above the canopy were common during the breeding period, while frugivores-insectivores and insectivores that feed at all forest strata characterized the non-breeding period. Out of 112 species registered, at least 10 are of conservation concern for Argentina, 14 are uncommon in the Neotropics, and 31 are migrants, highlighting the role of premontane forests for regional conservation. Most (c. 75%) premontane forests have already disappeared or are largely degraded. This situation calls for a rapid shift in regional policies, only possible if government, landowners, NGO's and academic institutions can share the common goal of habitat protection. *Accepted 1 April 2005*.

Key words: Andes, Argentina, feeding guild, montane forest, seasonal variation, species composition, species turnover.

INTRODUCTION

Tropical Andean forests contain high biodiversity (Churchill et al. 1995, Brown & Kappelle 2001), particularly of birds (Haffer 1987, Fjeldså 1995, Stotz et al. 1996). Bird community structure (e.g., species diversity, composition and abundance) and spatial distribution has rarely been studied in Andean forests at the mesoscale (1000's km²). High bird diversity of Andean forests, difficult access to many well-preserved forested sites within a region, and limited economic and human resources have largely prevented such studies. However, this scale of analysis is relevant because it is compatible with current conservation strategies (e.g., reserve size), and it may help understand how bird communities are influenced by variations in spatial and environmental conditions of the landscape. In this study, we describe the avifauna of 2000 km² of premontane Andean forests in Argentina.

Premontane forests, located at the base of forested mountain ranges along the Andes, represent the most endangered forest type of the Andean region (Stotz et al. 1996, Brown et al. 2001). This is due to a massive replacement of forested areas by agriculture, coupled with a narrow original distribution of this forest type. In Argentina, premontane forests origi-

nally occupied one third (c. 1 million ha) of Andean forests, but now only 20-30% remains forested, and what is left is being rapidly deforested (Grau & Brown 2000). The disappearance of premontane forests is of great concern because complete elevational forest gradients may be needed for maintaining species diversity over the long term (Kappelle & Brown 2001). This is particularly critical for bird species which have been shown to perform seasonal movements across many Neotropical montane-forest gradients (Terborgh 1974; Loiselle & Blake 1991, 1992; Winker et al. 1997). If part of the avifauna is temporally present at premontane forests and seasonally uses other elevational levels (i.e., elevational migrants), then the disappearance of the lower end of the gradient may also cause disruptions at montane areas (Stiles 1988, Blake & Loiselle 2000). Other species potentially affected by the disappearance of premontane forests are latitudinal and migrants, short-distance species restricted distribution, species with low regional abundance, and species of special conservation concern such as game birds or pets. For example, the Military Macaw (Ara militaris), a species of global conservation concern (CITES, Appendix 1), disappeared from Andean premontane forests of Argentina,

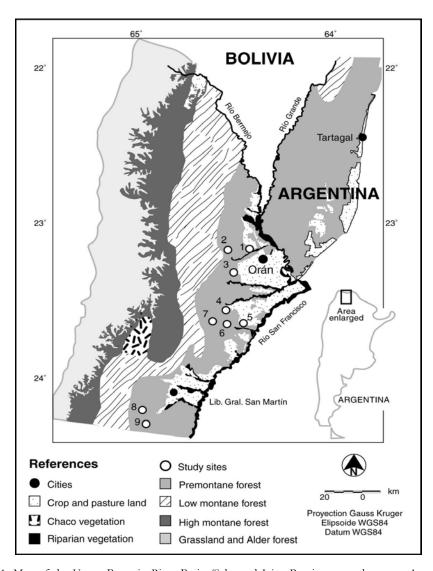


FIG. 1. Map of the Upper Bermejo River Basin (Salta and Jujuy Provinces, northwestern Argentina), showing study sites and environmental units. Study sites: (1) Finca Abra Grande (flat, 430 m, 23°06'S, 64°25'W), (2) Finca El Oculto (foothill, 600 m, 23°05'S, 64°32'W), (3) Finca El Tabacal (foothill, 550 m, 23°13'S, 64°28'W), (4) Colonia Santa Rosa (flat, 500 m, 23°23'S, 64°32'W), (5) Finca Urundel (flat, 390, 23°29'S, 64°25'W), (6) Finca Urundel (foothill, 500 m, 23°28'S, 64°29'W), (7) Finca Urundel (foothill, 660 m, 23°26'S, 64°33'W), (8) Finca Yuchán (foothill, 730 m, 23°52'S, 64°55'W), (9) Colonia Guayacán (foothill, 630 m, 24°00'S, 64°53'W). Map modified from Grau & Brown (2000).

and several others, such as the Toco Toucan (Ramphastos toco) and the Giant Antshrike (Batara cinerea), already reduced their latitudinal

range by ≥ 150 km (pers. observ.). Thus, many species may become regionally extinct as premontane forests continue to vanish.

The specific objectives of this study were fourfold. First, we described bird communities in terms of seasonal changes in species composition and abundance. We expected bird communities composed by large proportion of migrants, considering the marked seasonal changes in climatic conditions and forest phenology that characterize premontane forests (Malizia 2001), and the high mobility of birds shown for other mountain areas (Loiselle & Blake 1991, Winker et al. 1997). Second, we analyzed changes in species composition and abundance in relation to topography, elevation, and distance among sites. As a first approximation, premontane forests in Argentina can be divided into flat and foothill forests based on topography and elevation. This division may have biological relevance because most avian communities change along elevational gradients (Terborgh 1977, Young et al. 1998, Blake & Loiselle 2000, Kessler et al. 2001), even for short elevational ranges (c. 300 m) (Poulin et al. 1993, Patterson et al. 1998). We expected high rates of species turnover between flat and foothill forests and low rates among sites within the same forest type. Third, we examined bird community patterns considering feeding guilds in order to highlight functional aspects and to facilitate comparisons with studies conducted in other premontane areas, where species composition may differ. Finally, we determined the importance of premontane forests to regionally threatened species, uncommon species, and migrant birds.

MATERIALS AND METHODS

Study area. This study was conducted in premontane forests of the Upper Bermejo River Basin, provinces of Jujuy and Salta, northwestern Argentina (23°–24°S, Fig. 1). Premontane forest is the lowest elevation (400–700 m) forest type of Andean montane forests (400–2500 m) and is known as Selva

Tucumano-Boliviana (Cabrera 1976). This forest type ranges from Santa Cruz department in Bolivia (19°S) south to Tucumán province in Argentina (28°S). From an ornithological perspective, the study area lies in the Santa Cruz-Tucumán subregion, of the Central Andes region (Stotz et al. 1996). A detailed description of premontane forests can be found in Prado (1995) and Brown et al. (2001). As previously mentioned, premontane forests can be subdivided into "flat forests", located at the base of the Andes over relatively flat areas at c. 400–500 m, and "foothill forests", located along the eastern slopes of the mountains, between c. 500–700 m.

Climate in the study area is highly seasonal. Dry and cool weather (winter) occurs from May to September, while wet and hot conditions (summer) last from November to March. Total annual rainfall averages c. 1000 mm (Bianchi & Yañez 1992), and is concentrated (75–80%) during the summer (Hunzinger 1995). Mean annual temperature averages 21.5° C (Marmol 1995).

Fieldwork was conducted between April 2000 and October 2001. April to June samples correspond to the non-breeding season, whereas October to January samples correspond to the breeding season. We sampled nine premontane-forest sites (Fig. 1); six sites were sampled once (sites 3-4 and 6-9) and three sites were sampled twice (sites 1, 2 and 5), totaling 12 samples, six during each season (sites 1-6 during the non-breeding season, and sites 1, 2, 5, 7-9 during the breeding season). In this study we treat the 12 samples as independent samples, although if strictly we visited nine sites corresponding to 12 samples, because the three sites visited twice were sampled only once during the breeding season and once during the non-breeding season. Out of the nine sites, five were located in foothills and four in flat areas (Fig. 1).

Bird sampling. We used three sampling meth-

ods to survey bird communities to overcome limitations and biases of individual techniques (Bibby et al. 2000). We used point counts during both the breeding and non-breeding seasons, line transects only during the breeding season, and mist nets only during the nonbreeding season. At each site, we sampled the avifauna of a relatively small area (≤50 ha). Although differences in sampling methods used between seasons call for a careful interpretation of results, we consider that our seasonal comparisons provide useful information about bird community structure. We focused our study on all diurnal species that compose local communities at premontane forests. We established our study sites in forest-interior and relatively well-preserved areas. We followed Remsen et al. (2004) for systematic and taxonomic arrangements and for English common names (Appendix 1).

Point counts. We established 12 point-count stations at each site visited during the breeding season and 10 point-count stations at each site visited during the non-breeding season. We used only the first 10 point counts per site in analyses that required equal sample sizes (i.e., seasonal comparisons). All point counts were established at > 150-m intervals in forest-interior transects. All birds seen or heard in a 50-m radius were counted for 10 min at every point (72 points during the breeding season and 60 points during the non-breeding season). Each point count was visited only once. All counts were conducted for 2.5 h starting at sunrise

Line transects. During the breeding season, at each site, we surveyed 10 line transects distributed as uniformly as possible over a 50-ha forest-interior plot located at least 200 m from forest edges and roads, and from other transects. At each transect we recorded all species seen or heard without restriction of distance from the observer. Each transect was

walked at a slow and steady pace during a 30-min period (totaling 5 h per site and 30 h for the breeding season), without restriction of transect length. Since our objective was to detect as many bird species as possible, line transects were surveyed at different times during the day.

Mist nets. We used ground-level mist nets (12 m x 2.8 m, 36-mm mesh) during the non-breeding season, when some species are less likely to be singing and therefore to be detected by point-counts or transect methods. At each site, 15 mist nets were placed at > 40-m intervals along forest-interior transects. Mist nets were operated during three consecutive days at each site; the first two days for about 10 h/day and the third day for about 5 h, always starting right after dawn. All birds were banded with numbered aluminum leg bands and released close (~ 150 m) to mistnet locations to prevent disturbance at the nets.

Feeding guilds. We assigned bird species to feeding guilds (Appendix 1) based on a combination of three attributes: 1) main food type in the diet (carnivore, frugivore-insectivore, granivore, granivore-insectivore, insectivore, nectarivore, and omnivore), 2) forest strata where birds forage (ground, understory, canopy, all forest strata, above the canopy, and forest edge), and 3) primary foraging substrate from which food is obtained (air, air-foliage, bark, foliage, and ground) (Blake & Rougès 1997, Giannini 1999, Rougès & Blake 2001, L. R. Malizia & P. G. Blendinger pers. observ.).

Data analyses. We used Bray-Curtis ordination analyses to graphically compare similarity in species composition among communities (PC-ORD version 4.01, McCune & Mefford 1999). We used the variance-regression approach for endpoint selection and the Sørensen-distance measure for all analyses.

Bray-Curtis ordinations were based on presence-absence data of species recorded with all sampling methods. Ordination results based on species abundance are not presented because they were very similar to those obtained with presence-absence data. We used number of species per guild to assess similarity in guild composition among communities; the use of presence-absence data of guilds per site was precluded because most guilds were present at all sites.

We used number of species recorded at each site (combining all sampling methods) to analyze differences in species richness between seasons and forest types. Additionally, we estimated total species richness per site based on abundance data from point counts using EstimateS MMMean method with 1000 randomizations (Colwell 2000). These estimations tended to underestimate species richness per site when compared with total number of species recorded considering all methods (point counts, transects and mist nets), but provided similar results in comparisons between breeding and non-breeding periods, and between flat and foothill forests. Therefore, we do not include here results based on estimations of species richness.

We analyzed bird-species abundance considereding the number of individuals recorded with point counts (i.e., not considering mist nets or transects) because they were used at all sites. We assigned birds to categories of relative abundance for the mesoscale (premontane forest) and for the Neotropics based on our data and on Parker et al. (1996), respectively (Appendix 1). We used one-way analysis of variance (ANOVA) to test for differences in mean bird abundance per site (all species considered together) within breeding and non-breeding communities. Differences in mean bird abundance and species richness between seasons and forest types were analyzed with two-sample t-tests and Chi-square tests. We analyzed the relationship between species abundance and frequency (i.e., number of sites occupied), and resident and migrant bird abundance with correlations. Prior to the analyses we tested the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene test) and used non-parametric tests whenever the assumptions were not met.

Species turnover was estimated using the Sørensen coefficient of dissimilarity (Vellend 2001), and was calculated as $S_D = 1 - (c/\alpha)$, where c is the number of species shared by two communities and α is average number of species in each community. Values of S_D range from 0, indicating that every species found in one community is also found in the other one, to 1, indicating no species in common. We analyzed the relationship between species turnover and geographic distance with Mantel's tests using 9999 permutations to estimate r and P values, because regular r² and P values are not recommended due to the non-independence of the data (Legendre & Legendre 1998). Mantel's tests were performed using Passage version 1.1 (Rosenberg 2003).

RESULTS

Species richness. We recorded 112 species, ranging from 37 to 57 species per site (Appendix 1). Study sites were forest-interior and relatively well-preserved areas; therefore, we mainly recorded forest-interior birds. However, we also recorded several non-forest species [e.g., Striped Cuckoo (Tapera naevia), Great Kiskadee (Pitangus sulphuratus), Rufouscollared Sparrow (Zonotrichia capensis), Redcrested Finch (Coryphospingus cucullatus), and Shiny Cowbird (Molothrus bonariensis)], and several species that forage above the forest canopy [i.e., White-collared Swift (Streptoprocne zonaris), Sick's Swift (Chaetura meridionalis), Swallow-tailed Kite (Elanoides forficatus), Plumbeous Kite (Ictinia plumbea), Black Vul-

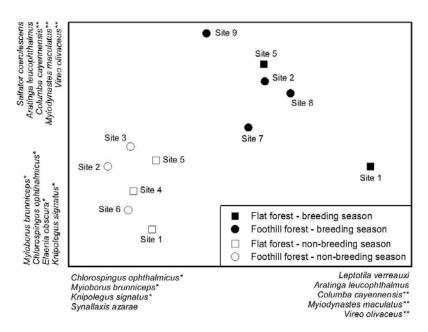


FIG. 2. Bray-Curtis ordination of bird communities based on presence/absence of species. Species most strongly correlated with the first two axes are indicated. *Elevational migrants, **Latitudinal migrants.

ture (*Coragyps atratus*), and Turkey Vulture (*Cathartes aura*)]. Mean number of species per site differed between seasons (two-sample t-test for unequal variances = 2.82, df = 6.8, P = 0.03), with more species during the breeding (mean = 49.8, range: 37–57) than the non-breeding period (41.0, 37–47). Accordingly, considering all sites combined per season, we found more species in premontane forests during the breeding season (93 vs 66 species; $\chi^2 = 4.25$, df = 1, P = 0.03).

We found no differences in mean species richness per site between flat (43.8, 37-51) and foothill (46.6, 37-57) forests (two-sample t-test for equal variances = -0.67, df = 10, P = 0.52). Considering all sites combined per forest type, we found similar numbers of bird species in flat (N = 89) and foothill forests (N = 96).

Seasonal changes in species composition. As previously mentioned, premontane-forest bird

communities showed important seasonal differences in species composition. Although many species (47) were present both during the breeding and non-breeding seasons, a high proportion of species (58%) were exclusive to one season, with 46 species exclusive to the breeding season and 19 to the nonbreeding season. Migrant species represented 27% (31 species) of the premontane forest avifauna, with 19 latitudinal and 13 elevational migrant species (Appendix 1). From this, Slaty Thrush (Turdus nigriceps) performs latitudinal and elevational movements and therefore was included in both migrant categories. Twenty migrant species were registered during the breeding season (18 latitudinal and 3 elevational migrants) and 18 species during the non-breeding season (6 latitudinal and 13 elevational migrants).

The first two axes of a Bray-Curtis ordination largely separated sites in relation to sampling season (Fig. 2). The ordination

TABLE 1. Analyses of variance of bird abundance per point count in breeding and non-breeding assemblages. Sites with distinct superscript letters showed significant differences (Tukey test of multiple comparisons, P < 0.05). See Figure 1 for site references.

Seasons	Sites									
Breeding	Site 1	Site 5	Site 2	Site 7	Site 8	Site 9				
$F_{5,66} = 10.95, P < 0.001$	(flat)	(flat)	(foothill)	(foothill)	(foothill)	(foothill)				
(12 counts/site)	9.7^{ab}	16.9^{bc}	13.2^{ab}	14.0^{b}	6.7^{a}	23.3°				
Non-breeding	Site 1	Site 4	Site 5	Site 2	Site 3	Site 6				
$F_{5,54} = 1.46, P = 0.22$	(flat)	(flat)	(flat)	(foothill)	(foothill)	(foothill)				
(10 counts/site)	10	13	18.1	16.1	12.1	12.3				

accounted for 63.2% of the variation in species composition across sites (axis I: 39.7%, axis II: 23.5%). Study sites were mainly grouped on the basis of species exclusive to each season, which included several migrant species (Fig. 2). Elevational migrants characterized the non-breeding season, while latitudinal migrants characterized the breeding season (Fig. 2).

Spatial distribution of species. Only 10 species out of 112 were present at all sites: two non-passeriforms [Tataupa Tinamou (Crypturellus tataupa) and Green-cheeked Parakeet (Pyrrhura molinae)] and eight passeriforms [Variable Antshrike (Thamnophilus caerulescens), Ochrecheeked Spinetail (Synallaxis scutata), Olivaceous Woodcreeper (Sittasomus griseicapillus), Plush-crested Jay (Cyanocorax chrysops), Rufous-bellied Thrush (Turdus rufiventris), Saffron-billed Sparrow (Arremon flavirostris), Tropical Parula (Parula pitiayumi), and Twobanded Warbler (Basileuterus bivittatus)]. Twenty-two bird species were recorded at only one site, including one species of ibis, vulture, guan and hummingbird, two species of cuckoos, three of diurnal raptors, and 13 passeriform species (Appendix 1).

Most species (72 out of 112) were present in both flat and foothill areas. Seventeen were registered only in flat sites, and 23 were exclusive to foothill sites. However, more than half of these species (22 out of 40) were rare (i.e., present at only one site), and therefore were inadequate to characterize flat or foothill forests

Species turnover. Mean dissimilarity in species composition across all site pairs was 0.41, indicating intermediate levels of species turnover among bird communities. As expected, mean dissimilarity between sites sampled during the same season was lower (0.31) than for sites sampled during different seasons (0.50) (two-sample t-test = 11.9, df, corrected to account for non-independence of pairs, = 12, P < 0.001), indicating the temporal turnover in species composition across seasons. Comparing seasons, mean dissimilarity was higher during the breeding (0.36) than the nonbreeding (0.26) period (two-sample t- test for equal variances = 4.56, df = 28, P < 0.001), suggesting more homogeneous spatial distributions of birds during the non-breeding period.

Turnover in species composition over the entire study area was not correlated with geographic distance between sites (Mantel's test, r = 0.08, P = 0.29). Considering each season separately, species turnover and distance were again unrelated (Mantel's tests: breeding season, r = 0.02, P = 0.43; non-breeding season, r = 0.23, P = 0.22). Mean dissimilarity among flat-forest sites (0.34) was slightly higher than among foothill sites (0.29). Mean dissimilarity between flat and foothill sites (0.31) was

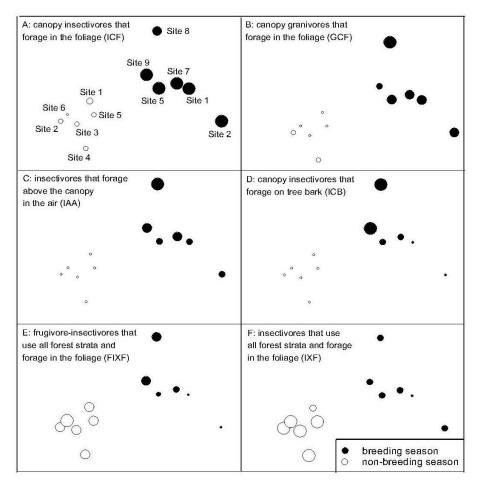


FIG. 3. Bray-Curtis ordinations of bird communities based on number of species per feeding guild. Circles' size is proportional to the number of species per feeding guild present at each community.

intermediate to the previous values, instead of higher as we expected from comparisons of different forest types.

Species abundance. Bird abundance was estimated at 132 point counts in which we registered 1819 individuals corresponding to 88 species (Appendix 1). Total number of individuals per species was correlated with the number of sites occupied, i.e., species that were more abundant tended to be present in more communities ($r_s = 0.46$, N = 88, P <

0.001).

Mean bird abundance per point count did not differ between seasons (two-sample t-test = 0.02, df = 10, P = 0.32) or between forest types (two-sample t-test = 0.50, df = 10, P = 0.21). During the breeding season, mean bird abundance per point count differed among sites (Table 1), due both to the presence of migrant and resident birds. Latitudinal migrants represented in average 26.7% of the birds recorded per site during the breeding season, ranging among sites from an average

of 2.2 to 7.9 individuals per point count. The number of resident birds also varied markedly among sites ($F_{5,66} = 10.27$, P < 0.001), but mean abundance of resident and migrants species were not correlated (r = 0.70, N = 6, P = 0.11). In contrast to the breeding season, there were no differences among sites in mean bird abundance per point count during the non-breeding season (Table 1). Elevational migrants represented in average 14.9% of the birds recorded per site during the non-breeding season, ranging among sites from an average of 0.8 to 4.1 individuals per point count.

Feeding guilds. Combining data of primary foraging substrata, foraging forest strata, and diet, we classified the 112 bird species recorded in premontane forests into 35 feeding guilds (Appendix 1). Due to our detailed guild classification, most guilds included one or a few species, and only four guilds included seven or more species: canopy insectivores that capture prey in the foliage (11), understory insectivores that capture prey in the foliage (9), canopy insectivores that capture prey both in the foliage and the air (7), and forestedge granivore-insectivores that forage in the foliage (7).

The results of a Bray-Curtis ordination based on feeding guilds explained 52.2% of the variation and separated breeding from non-breeding communities (axis I: 36%, axis II: 16%). Six feeding guilds, which included 34 species (13 migrants), explained most of the differences among seasons ($\chi^2 = 25.4$, df = 5, P < 0.001; Fig. 3). The breeding season was characterized by bird species that forage in or above the canopy. They included i) medium and high forest-strata insectivores, such as Streaked Flycatcher (Myiodynastes maculatus), Green-backed and White-winged becards (Pachyramphus viridis and P. polychopterus, respectively), Black-capped Antwren (Herpsilochmus atricapillus), Red-eye Vireo

(Vireo olivaceus), and Tropical Parula (Fig. 3a); ii) canopy granivores, such as Golden-collared Macaw (Propyrrhura auricollis), White-eyed Parakeet (Aratinga leucophthalma), Green-cheeked Parakeet (Pyrrhura molinae), Scally-headed Parrot (Pionus maximiliani), Blue-fronted Parrot (Amazona aestiva), and Pale-vented Pigeon (Columba cayennensis) (Fig. 3b); iii) insectivores that forage above the canopy, such as Whitecollared and Sick's Swifts, Swallow-tailed and Plumbeous Kites, and Tropical Kingbird (Tyrannus melancholicus) (Fig. 3c); and iv) canopy insectivores that forage on tree bark, such as Golden-olive and Cream-backed woodpeckers (Piculus rubiginosus and Campephilus leucopogon, respectively), Stripe-crowned Spinetail (Cranioleuca pyrrhopia), and Streaked Xenops (Xenops rutilans) (Fig. 3d). In contrast, the nonbreeding season was characterized by bird species that used all vegetation strata, from understory to canopy. They included i) frugivore-insectivores, such as Dusky-legged Guan (Penelope obscura), Slaty, Rufous-bellied and Creamy-bellied thrushes (Turdus nigriceps, T. rufiventris and T. amaurochalinus, respectively), Common Bush-tanager (Chlorospingus ophthalmicus), and Sayaca Tanager (Thraupis sayaca) (Fig. 3e); and ii) insectivores, such as Mottledcheeked Tyrannulet (Phylloscartes ventralis), Buff-browed Foliage-Gleaner (Syndactyla rufosuperciliata), Brown-capped Redstart (Myioborus brunniceps), and Rusty Flowerpiercer (Diglossa sittoides) (Fig. 3f).

Common vs uncommon species. Using the abundance assessments for Neotropical birds published by Parker et al. (1996), we recorded 50 species as common, 48 as fairly common and 14 as uncommon (Appendix 1). At the mesoscale, considering all premontane forests sites together, we found 23 uncommon species (i.e., species present only at one site per seasons and with ≤2 individuals recorded at point counts), most (16) of them during the breeding season (Appendix 1). The Hepatic

Tanager (Piranga flava) was the only uncommon species recorded during both seasons, although the number of uncommon species present year round was probably underestimated, since uncommon species are by definition hard to detect and could be lost during short-term sampling periods. Most (79%) latitudinal and elevational migrants were common species, suggesting that premontane forest harbored large populations of these migrants, and reinforcing the importance of premontane forests for their conservation. Uncommon migrants included two elevational migrants specialized in nectar [Planalto Hermit (Phaetornis pretrei) and Rusty Flowerpiercer], a resource patchily distributed and scarce during the non-breeding season. The other uncommon migrant species were insectivorous latitudinal migrants mainly related with more open environments [Dark-billed Cuckoo (Coccyzus melacoryphus), Plumbeous Kite, White-winged Black-Tyrant (Knipolegus aterrimus), Tropical Kingbird, and Variegated Flycatcher (*Empidonomus varius*)].

DISCUSSION

To our knowledge, this is the first study to report abundance, composition and diversity of bird communities at premontane forests, which cover 2.5 million ha of the Santa Cruz-Tucumán subregion. Despite the limitations of this study, that include modest sample size at each site, it may well represent the most detailed report currently available to guide regional conservation strategies.

This study showed important seasonal changes in bird-species richness and composition, in part due to the arrival of migrants. More speciose communities were recorded during the breeding than the non-breeding season, although total bird abundance did not vary between periods. However, we registered more individuals and species of migratory birds during the breeding season. Breeding

assemblages were characterized by the presence of latitudinal migrants, e.g., Sick's Swift, Pale-vented Pigeon, Euler's Flycatcher (*Lathrotriccus euleri*), three *Myiarchus* flycatchers, Streaked Flycatcher, Red-eye Vireo, and Swainson's Thrush (*Catharus ustulatus*), while non-breeding assemblages harbored elevational migrants, e.g., Red-tailed Comet (*Sappho sparganura*), Buff-banded Tyrannulet (*Mecocerculus hellmayri*), Andean Tyrant (*Knipolegus signatus*), Brown-capped Redstart, Common Bush-Tanager, and Black-backed Grosbeak (*Pheucticus aureoventris*).

We found no significant differences in bird species richness, composition or abundance in relation to elevation and topographic location (i.e., flat vs foothill) within premontane forest. Flat-forest sites were not characterized by any particular set of species, in part due to the patchy distributions of birds across the entire study area. If this pattern holds after detailed studies, both an encouraging and a warning message should be stated. The encouraging message is that no bird species seems to depend exclusively on flat premontane forest, the most endangered habitat of this part of the Andean region. The warning message is that we know little about the interdependence of flat and foothill premontane forests in terms of diversity and functional aspects. If complete elevational gradients are needed to maintain the diversity of Andean forests (see below), then the rapid destruction of flat forests may hamper all efforts of habitat conservation in the region.

Species turnover between communities ranged from intermediate (0.50, different seasons) to low values (0.26, within the non-breeding season) in absolute terms, but was relatively high considering that all sites where sampled within limited latitudinal (100 km) and elevational ranges (390–730 m). Our results are similar to those of Poulsen & Krabbe (1998) for other Andean forests, where they interpreted low dissimilarity values

(mean = 0.33) as evidence of moderately high differences in bird species composition. In our study, geographical distance did not explain dissimilarity in species composition between communities, as suggested by nonsignificant correlations between inter-site distance and species turnover. Environmental factors, such as forest type, neither explain such dissimilarities. We do not think the dissimilarity levels found are a consequence of our sampling methods. This idea is supported by extra observations conducted during the breeding season, when we made an extra effort to register all birds present at each site, besides the systematic methods presented here. This initiative showed that our sampling methods detected on average 88% of all birds presented at each site. This result supports the notion that we sampled a high percentage of the species present at each site and that the dissimilarity levels found may be caused by patchily-distributed species at the mesoscale, a pattern also reported for other forest bird communities (Gaston & Blackburn 2000). The causes promoting patchy distribution of birds are unclear; it has been proposed that they are largely species specific and that the floristic structure and composition of the habitat may play an important role (Bierregaard & Stouffer 1997, Renjifo 2001). Although we sampled relatively well-preserved sites (no fragments were considered, see Fig. 1), the characteristics of the matrix around each site varied largely due to forest degradation and transformation. Perhaps environmental variables acting at small (e.g., 0.1 km²) and landscape scales (e.g., 100 km²) may have been responsible for the amount of species turnover found.

The spatial distribution of feeding guilds did not show any specific pattern, but the temporal distribution did reveal interesting seasonal differences. The breeding period was characterized by insectivorous and granivorous species that primarily forage in or above the canopy, while the non-breeding season was characterized by frugivore-insectivores and insectivores that move across all forest strata to feed. Premontane forests are highly seasonal in terms of leaf phenology, and most canopy trees lose their leaves during the dry and cold period. This may explain the virtual absence of feeding guilds that primarily forage in the canopy and the prevalence of guilds that utilize all strata during the non-breeding period.

Regional distribution and abundance of species can strongly influence the composition and structure of local communities. In premontane forest, species abundance and frequency (i.e., sites occupied) were correlated, indicating that regionally abundant species also tended to occupy many local communities. This seems to be a general rule for temperate and subtropical areas (e.g., Blackburn & Gaston 2001), but probably not for tropical areas where many narrowly distributed species may show high abundance within their small ranges. In our case, all but one (Ochre-cheeked Spinetail) common species (i.e., 36 species with > 0.5% of total counts and present at more than 1 site per season) at premontane forests are also common or fairly common in the Neotropics (sensu Stotz et al. 1996). Most (22/36) common species at premontane forests also tend to occupy large areas in South America (> 1/ 4 of the continent), and only some (6/36)have relative small (< 1/8) continental distributions [Green-cheeked Parakeet, Ochrefaced Tody-Flycatcher (Poecilotriccus plumbeiceps), Azara's Spinetail (Synallaxis azarae), Two-banded Warbler (Basileuterus bivittatus), Common Bush-Tanager, and Black-backed Grosbeak] (Ridgely & Tudor 1989, 1994; del Hoyo et al. 1992, 1997, 1999, 2001).

In this study, we found that at least 10 species of birds inhabiting premontane forests may be threatened in one or several ways for Argentina. The Toco Toucan, Giant Ant-

shrike (P. Capllonch com. pers.) and Hookbilled Kite (Blendinger et al. 2004) contracted their distribution range during the last decades. The Dusky-legged Guan is heavily hunted for food, while the Blue-fronted Parrot and Black-backed Grosbeak are widely used as pets in legal and illegal markets. The premontane forest may represent an important habitat for elevational migrant species restricted to montane forest during the breeding season, such as the Andean Tyrant and the Buff-banded Tyrannulet. Several species restricted in Argentina to the Santa Cruz-Tucumán subregion are residents of premontane forests, such as the Dot-fronted Woodpecker (Veniliornis frontalis) and the Whitethroated Antpitta (Grallaria albigula). Moreover, the White-throated Antpitta, subspecies cinereiventris, is endemic to the study region (Jujuy and Salta) in Argentina (Chebez 1999). This list highlights the need for premontane forest to be included in a national conservation strategy.

In this study we recorded 112 bird species at Andean premontane forests, representing c. 11% of Argentina's bird diversity. From this, 10 species are of conservation concern for the country, 14 are uncommon for the Neotropics as a whole, and 31 are migrants, either latitudinal (19) or elevational (13). As previously mentioned, conservation concerns have increased in the last decades with accumulated evidence suggesting the importance of complete elevational forest gradients for maintaining bird species diversity at the long term in the Neotropics (Terborgh 1974, Stiles 1988; Loiselle & Blake 1991, 1992; Winker et al. 1997, Blake & Loiselle 2000). This information, coupled with premontane forest's endangered status (Stotz et al. 1996, Brown et al. 2001), call for the protection of this habitat. As a future challenge, we need to better understand the role of premontane forest at the regional scale as a key component for avian migrant movements, both to upper montane forests and to lowland forests as the Chaco thorny woodland.

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BIRDS OF ANDEAN PREMONTANE FORESTS

APPENDIX 1. List of species detected in Andean premontane forests of northwestern Argentina, including bird attributes (migrant status, feeding guild, Neotropical abundance, and premontane-forest abundance), number of individuals counted (considering 10 point counts per site; not mist nets or transects) at flat (ind. flat) and foothill (ind. hill) forests, and number of sites occupied (considering all methods) during breeding and non-breeding seasons. Number of sites sampled: breeding season, two flat and four foothill sites; non-breeding season, three flat and three foothill sites.

Species

Migr. Feeding Neotrop. Premon. Breeding Non-breeding

Species	Migr.	Feeding	Neotrop.	Premon.		Breeding		N	on-breedi	ng
	status ¹	guild ²	abund ³	abund.4	Ind. flat	Ind. hill	No. sites	Ind. flat	Ind. hill	No. sites
Tataupa Tinamou (Crypturellus tataupa)	R	GI.G.G	F	С	8	14	6	1	5	6
Dusky-legged Guan (Penelope obscura)	R	FI.X.F	F	U	0	0	1	0	0	0
Buff-necked Ibis (Theristicus caudatus)	R	I.G.G	F	U	0	0	1	0	0	0
Turkey Vulture (Cathartes aura)	R	C.A.G	С	С	0	0	2	0	0	0
Black Vulture (Coragyps atratus)	R	C.A.G	С	U	0	0	1	0	0	0
Hook-billed Kite (Chondrohierax uncinatus)	R	C.C.F	U	U	0	0	1	0	0	0
Swallow-tailed Kite (Elanoides forficatus)	L	I.A.A	U	С	0	2	2	0	0	0
Pumbeous Kite (Ictinia plumbea)	L	I.A.A	С	U	0	0	1	0	0	0
Gray Hawk (Asturina nitida)	5	C.C.F	F	U	0	0	1	0	0	0
Roadside Hawk (Buteo magnirostris)	R	C.C.F	С	С	0	1	4	0	0	3
Barred Forest-Falcon (Micrastur ruficollis)	R	C.X.A	F	С	0	0	3	0	0	0
Pale-vented Pigeon (Patagioenas cayennensis)	L	G.C.F	C	С	3	12	6	0	0	0
White-tipped Dove (Leptotila verreauxi)	R	G.G.G	С	С	0	0	5	0	0	0
Large-tailed Dove (Leptotila megalura)	R	G.G.G	U	С	0	8	4	0	0	4
Golden-collared Macaw (Propyrrhura auricollis)	R	G.C.F	F	С	0	6	4	0	0	0
White-eyed Parakeet (Aratinga leucophthalma)	R?	G.C.F	С	С	28	79	6	0	0	0
Green-cheeked Parakeet (Pyrrhura molinae)	R	G.C.F	С	С	4	33	6	6	44	6
Scally-headed Parrot (Pionus maximiliani)	R	G.C.F	F	С	1	2	4	1	0	2
Blue-fronted Parrot (Amazona aestiva)	R	G.C.F	F	С	6	6	4	21	8	6
Dark-billed Cuckoo (Coccyzus melacoryphus)	L	I.U.F	F	U	1	0	1	0	0	0
Squirrel Cuckoo (Piaya cayana)	R	O.X.F	С	С	0	1	2	0	0	0
Striped Cuckoo (Tapera naevia)	R	I.U.F	C	U	0	0	1	0	0	0
White-collared Swift (Streptoprocne zonaris)	R	I.A.A	F	C	0	0	2	0	0	0
Sick's Swift (Chaetura meridionalis)	L	I.A.A	C	C	7	1	4	0	0	0
Planalto Hermit (Phaethornis pretrei)	A	N.U.F	F	U	0	0	0	0	0	1
Glittering-bellied Emerald (Chlorostilbon aureoventris)	R	N.X.F	C	C	0	3	2	6	7	5

Species	Migr.	Feeding	Neotrop.	Premon.		Breeding		Non-breeding			
	status ¹	guild ²	abund ³	abund.4	Ind. flat	Ind. hill	No. sites	Ind. flat	Ind. hill	No. sites	
White-bellied Hummingbird (Amazilia chionogaster)	R	N.C.F	С	С	0	3	3	2	1	5	
Red-tailed Comet (Sappho sparganura)	Α	N.X.F	F	C	0	0	0	1	0	2	
Blue-tufted Starthroat (Heliomaster furcifer)	R	N.E.F	U	C	0	0	2	0	0	0	
Blue-crowned Trogon (Trogon curucui)	R	FI.C.F	F	C	0	2	5	4	4	6	
Blue-crowned Motmot (Momotus momota)	R	O.U.F	C	C	1	1	4	1	0	4	
Toco Toucan (Ramphastos toco)	R	O.C.F	F	С	0	0	2	0	0	0	
White-barred Piculet (Picumnus cirratus)	R	I.U.B	С	C	2	1	4	0	0	0	
Dot-fronted Woodpecker (Veniliornis frontalis)	R	I.U.B	С	C	0	0	3	1	3	5	
Golden-olive Woodpecker (Piculus rubiginosus)	R	I.C.B	F	С	0	3	4	0	0	0	
Cream-backed Woodpecker (Campephilus leucopogon)	R	I.C.B	U?	С	0	3	3	0	3	6	
Olivaceous Woodcreeper (Sittasomus griseicapillus)	R	I.X.B	С	C	19	28	6	7	11	6	
Great Rufous Woodcreeper (Xiphocolaptes major)	R	I.X.B	U	С	0	0	0	1	0	3	
Black-banded Woodcreeper (Dendrocolaptes picumnus)	R	I.X.B	U	C	2	2	4	0	1	6	
Narrow-billed Woodcreeper (Lepidocolaptes angustirostris)	R	I.X.B	F	C	2	7	6	0	1	2	
Sooty-fronted Spinetail (Synallaxis frontalis)	R	I.U.F	F	C	1	0	2	0	0	3	
Azara's Spinetail (Synallaxis azarae)	R	I.U.F	F	C	0	2	2	6	3	6	
Ochre-cheeked Spinetail (Synallaxis scutata)	R	I.U.F	U	С	12	17	6	18	17	6	
Stripe-crowned Spinetail (Cranioleuca pyrrhophia)	R	I.C.B	F	C	0	4	2	0	0	0	
Buff-browed Foliage-gleaner (Syndactyla rufosuperciliata)	R	I.X.F	C	С	10	26	5	20	41	5	
Streaked Xenops (Xenops rutilans)	R	I.C.B	F	С	5	0	3	0	0	0	
Giant Antshrike (Batara cinerea)	R	O.U.F	U	С	0	5	4	1	0	3	
Great Antshrike (Taraba major)	R	O.U.F	С	U	1	0	1	0	0	0	
Variable Antshrike (Thamnophilus caerulescens)	R	I.U.F	С	С	33	43	6	2	6	6	
Stripe-backed Antbird (Myrmorchilus strigilatus)	R	I.U.F	F	С	3	0	2	0	0	0	
Black-capped Antwren (Herpsilochmus atricapillus)	T5	I.C.F	C	С	18	25	5	1	0	2	
White-throated Antpitta (Grallaria albigula)	R	I.G.G	U	С	0	0	2	0	0	0	
Greenish Elaenia (Myiopagis viridicata)	R	I.U.AF	F	С	2	0	3	11	0	3	
Small-billed Elaenia? (Elaenia sp. [parvirostris?])	L	FI.X.AF	C	С	0	12	1	0	0	2	
Highland Elaenia (Elaenia obscura)	Α	FI.U.AF	U	C	0	0	0	1	1	4	

APPENDIX 1. Continued.

Species	Migr.	Feeding	Neotrop.	Premon.		Breeding		N	on-breed	ng
	status ¹	guild ²	abund ³	abund.4	Ind. flat	Ind. hill	No. sites	Ind. flat	Ind. hill	No. sites
Southern Beardless-Tyrannulet (Camptostoma obsoletum)	R	I.C.AF	F	С	0	1	2	0	0	0
Buff-banded Tyrannulet (Mecocerculus hellmayri)	Α	I.C.AF	F	С	0	0	0	2	2	4
White-throated Tyrannulet (Mecocerculus leucophrys)	Α	I.C.AF	C	С	0	0	0	6	0	2
White-crested Tyrannulet (Serpophaga subcristata)	R	I.E.AF	F	С	0	3	2	0	0	0
Mottled-cheeked Tyrannulet (Phylloscartes ventralis)	R	I.X.F	F	С	4	4	6	0	10	5
Sepia-capped Flycatcher (Leptopogon amaurocephalus)	Α	I.U.AF	F	C	0	1	2	6	3	5
Pearly-vented Tody-Tyrant (Hemitriccus margaritaceiventer)	R	I.U.F	C	С	3	8	2	0	0	0
Ochre-faced Tody-Flycatcher (Poecilotriccus plumbeiceps)	R	I.U.F	F	С	25	19	6	22	5	5
Yellow-olive Flycatcher (Tolmomyias sulphurescens)	R	I.C.AF	F	C	5	8	4	0	6	4
Euler's Flycatcher (Lathrotriccus euleri)	L	I.U.AF	F	С	13	3	4	0	0	1
Fuscous Flycatcher (Cnemotriccus fuscatus)	R	I.U.AF	F	U	0	0	0	0	0	1
Andean Tyrant (Knipolegus signatus)	Α	I.X.AF	U	C	0	0	0	0	5	5
White-winged Black-Tyrant (Knipolegus aterrimus)	L	I.E.AF	F	U	0	0	0	0	0	1
Great Kiskadee (Pitangus sulphuratus)	R	I.E.F	C	С	0	0	0	1	0	2
Streaked Flycatcher (Myiodynastes maculatus)	L	I.C.F	C	С	8	32	5	0	0	0
Variegated Flycatcher (Empidonomus varius)	L	I.C.A	F	U	1	0	1	0	0	0
Tropical Kingbird (Tyrannus melancholicus)	L	I.A.A	C	U	0	2	1	0	0	0
Rufous Casiornis (Casiornis rufus)	R	I.C.AF	F	С	0	0	0	1	0	4
Dusky-capped Flycatcher (Myiarchus tuberculifer)	Γ5	I.X.AF	C	C	0	5	4	0	0	0
Swainson's Flycatcher (Myiarchus swainsoni)	L	I.C.AF	F	С	1	3	3	0	0	0
Brown-crested Flycatcher (Myiarchus tyrannulus)	L	I.C.AF	F/C	С	1	3	4	1	0	1
Green-backed Becard (Pachyramphus viridis)	R	I.C.F	U/P	U	2	0	1	0	0	0
White-winged Becard (Pachyramphus polychopterus)	L	I.C.F	C	С	0	2	2	0	0	0
Rufous-browed Peppershrike (Cyclarhis gujanensis)	R	I.C.F	C	С	1	9	4	1	0	2
Red-eye Vireo (Vireo olivaceus)	L	I.C.F	C	C	20	26	6	0	0	0
Plush-crested Jay (Cyanocorax chrysops)	R	O.X.F	F	C	5	16	6	8	6	6
House Wren (Troglodytes aedon)	R	I.U.F	C	C	3	0	1	8	8	5
Spotted Nightingale-Thrush (Catharus dryas)	Α	FI.U.F	F	U	0	0	0	0	0	1
Swainson's Thrush (Catharus ustulatus)	L	FI.U.F	-	С	1	4	4	0	0	0

Species	Migr.	Feeding	Neotrop.	Premon.		Breeding		N	on-breedi	ing
	status ¹	guild ²	abund ³	abund.4	Ind. flat	Ind. hill	No. sites	Ind. flat	Ind. hill	No. sites
Slaty Thrush (Turdus nigriceps)	A,L	FI.X.F	F	С	0	2	2	2	1	5
Rufous-bellied Thrush (Turdus rufiventris)	R	FI.X.F	C	C	11	26	6	18	18	6
Creamy-bellied Thrush (Turdus amaurochalinus)	R	FI.X.F	С	C	0	1	2	3	1	3
Hooded Tanager (Nemosia pileata)	R	FI.C.F	F	U	2	0	1	0	0	0
Orange-headed Tanager (Thlypopsis sordida)	R	FI.U.F	F	C	0	2	1	0	0	3
Sayaca Tanager (Thraupis sayaca)	R	FI.X.F	С	С	8	16	4	9	54	5
Guira Tanager (Hemithraupis guira)	R?	FI.C.F	С	С	4	2	5	0	0	0
Chestnut-vented Conebill (Conirostrum speciosum)	R	I.C.F	С	С	1	2	6	2	0	1
Rusty Flowerpiercer (Diglossa sittoides)	A	I.X.F	F	U	0	0	0	0	0	1
Common Bush-Tanager (Chlorospingus ophthalmicus)	A	FI.X.F	С	C	0	0	0	17	46	6
Hepatic Tanager (Piranga flava)	R	FI.C.F	F	U	0	0	1	1	0	1
Rufous-collared Sparrow (Zonotrichia capensis)	R	GI.E.F	С	U	0	0	0	0	1	1
Black-capped Warbling-Finch (Poospiza melanoleuca)	R	GI.E.F	С	C	0	0	2	0	0	0
Dull-colored Grassquit (Tiaris obscurus)	R?	GI.E.F	U/P	C	0	0	0	0	0	2
Saffron-billed Sparrow (Arremon flavirostris)	R	GI.U.F	F	С	7	19	6	28	24	6
Stripe-headed Brush-Finch (Buarremon torquatus)	R	GI.U.F	С	C	0	5	3	0	0	1
Red-crested Finch (Coryphospingus cucullatus)	R	GI.E.F	С	С	0	0	0	0	0	2
Black-backed Grosbeak (Pheucticus aureoventris)	A	GI.C.F	С	С	0	2	1	13	0	3
Grayish Saltator (Saltator coerulescens)	R	GI.E.F	С	C	1	3	3	0	0	0
Ultramarine Grosbeak (Cyanocompsa brissonii)	R	GI.E.F	F	U	0	1	1	0	0	0
Tropical Parula (Parula pitiayumi)	R	I.C.F	С	С	11	42	6	49	59	6
Brown-capped Redstart (Myioborus brunniceps)	A	I.X.F	F	C	0	0	0	2	6	6
Two-banded Warbler (Basileuterus bivittatus)	R	I.U.F	F	С	9	49	6	32	50	6
Crested Oropendola (Psarocolius decumanus)	R	O.C.F	C/P	С	0	5	2	1	0	2
Epaulet Oriole (Icterus cayanensis)	R	I.C.F	F	С	0	0	0	2	0	2
Shiny Cowbird (Molothrus bonariensis)	R	GI.E.F	С	U	0	0	1	0	0	0
Purple-throated Euphonia (Euphonia chlorotica)	R	FI.C.F	С	С	3	7	5	4	2	6
Golden-rumped Euphonia (Euphonia cyanocephala)	R	FI.C.F	F/P	U	0	0	1	0	0	0

¹Migrant status: A = elevational migrant, L = latitudinal migrant, R = resident.

²Feeding guilds: composed as a combination of three categories separated by dots. i) The first set of letters refers to diet: C = carnivore, FI = frugivore-insectivore, G = granivore, GI = granivore-insectivore, I = insectivore, N = nectarivore, O = omnivore. ii) The second set of letters refers to forest strata where birds forage: A = above the canopy, C = canopy, E = forest edge, G = ground, U = understory, X = all forest strata. iii) The third set of letters refers to foraging substrate from where food is obtained: A = air, AF = air-foliage, B = bark, F = foliage, G = ground.

³Neotropical abundance (sensu Parker et al. 1996): C = common, F = fairly common, P = patchily distributed, U = uncommon.

⁴Premontane-forest abundance (at the mesoscale): C = common, U = uncommon.