VARIATION IN CAPTURE RATES OF UNDERSTORY BIRDS IN EL REY NATIONAL PARK, NORTHWESTERN ARGENTINA

John G. Blake^{1, 2} & Mercedes Rougès^{1, 2}

¹ Department of Biology, University of Missouri-St. Louis, St. Louis, MO, 63121, U.S.A. ² Laboratorio Investgaciones Ecológicas de las Yungas, Tucumán, Argentina.

Abstract. Montane forests located in northwestern Argentina are important areas for conservation but have received little study. We used mist nets in a preliminary survey of understory birds at El Rey National Park, Salta; the park encompasses 44,162 ha over an altitudinal range from 700 to 2300 m. Study sites were at two elevations representing distinct forest types: Selva Basal (SB; 900–1200 m) and Selva de Mirtaceas (SM; 1200–1600 m). Birds were sampled during the dry and wet seasons 1994 and during the dry season 1996. We captured 660 birds (359 in SB; 301 in SM) representing 42 species (38 in SB; 31 in SM). Number of species per sample ranged from 17 to 27 but differences were largely due to difference in number of captures. Considerable variation in capture rates was noted between seasons and elevations. Importance of fruit in the diet was substantially greater during the wet season. Accepted 22 August 1997.

Key words: Argentina, diet, elevational gradient, fruit, migrant, mist net, montane forest.

INTRODUCTION

Most studies on structure of bird communities have been conducted in northern temperate areas and, to a much lesser extent, in tropical regions of Central and northern South America. Relatively little is known about bird community structure in subtropical habitats of the southern hemisphere. Similarly, most research on migrants has been conducted in northern hemisphere habitats with less attention given to "austral" migrants (Marantz & Remsen 1991, Chesser 1994, Stotz et al. 1996). Comparative studies on the importance of latitudinal and altitudinal movements (and similar scale movements) and diet shifts in structuring bird populations are generally lacking from subtropical sites in the southern hemisphere. Given that many species in subtropical montane forests may undergo altitudinal movements (Vides 1992), it is clear that additional studies on these systems are needed.

Montane forests, or "yungas", reach their southernmost extent in a series of isolated reserves in northwestern Argentina. These forests are important areas for conservation but have received little ecological research (e.g., Brown 1986). We initiated this study to obtain a preliminary description of variation in distribution, composition, abundance, and diets of understory bird species along an elevational gradient of montane forests in one of these isolated reserves (El Rey National Park). More specifically we address the question of how capture rates of understory birds differ between forests at two elevations and between dry (winter, nonbreeding) and wet (summer, breeding, period of fruit abundance) seasons and how diets differ among species and between seasons. Results presented here are based on samples from two dry seasons but only one wet season; thus, interpretation of observed patterns must be considered tentative and require further substantiation. Nonetheless, the data do provide a preliminary assessment of variation in bird communities in a poorly studied region.

STUDY SITE

Argentinean montane forests are located on the eastern slopes of a series of discontinuous mountain ranges separated by more arid intermountain valleys (Brown & Ramadori 1989). These forests typically receive from 1000 to 3000 mm annual precipitation (Bianchi 1981) although long-term records are lacking. Precipitation is concentrated during November to April (summer and fall) when about 80 % of the total annual precipitation occurs. The climate is subtropical with a mean annual temperature of 20 °C (Chalukian 1991); frost and even snow are not uncommon in some areas, particularly at higher elevations.

We conducted this research at El Rey National Park (24° 45' S 64° 40' W), Salta, Argentina. El Rey was created in 1948 and encompasses 44,162 ha over an altitudinal range from 700 to 2300 m. Study sites were located at two elevations that represent two distinct forest types: Selva Basal (900-1200 m) and Selva de Mirtaceas (1200-1600 m) (Brown 1986). Selva Basal replaces lower elevation transition (between dry chaco and humid forest) forest; it is typically taller with a more developed understory than the lower forest. The canopy is dominated by Cinnamomum (Phoebe) porphyria, Blepharocalix gigantea, Cedrella lilloi, and C. angustifolia. A second stratum is composed of species typically less than 20 m, such as Allophyllus edulis, Zanthoxylum (Fagara) coco, and Prunus tucumanensis. In the understory (2-5 m), Chusquea lorentziana, Urera baccifera, Miconia ioneura, and several shrubs in the Solanaceae family are common. Epiphytes are abundant, particularly bromeliads.

At higher elevations (above 1200 m) Selva Basal is replaced by Selva de Mirtaceas, a forest dominated by trees in the Mirtaceae family (Myrcianthes mato, M. pseudomato, Blepharocalix gigantea, Eugenia uniflora, E. pungens, and Myrrhinium lorathoides). In the understory, Piper tucumanum, Celtis sp., Pteris deflexa, Polystichum planthyphyllum, Aphelandra hieronimy, and Justicia sp. are most common. Epiphytes are also an important element in this forest. Selva de Mirtaceas is replaced at higher elevations by forest typically dominated by Podocarpus and/or Alnus and grasslands.

Fruit production reaches a peak (number of species in fruit) in both Selva Basal and Selva de Mirtaceas forests during November-January, generally coinciding with the peak in rainfall (Brown 1986). The main breeding period for birds is between October-December (pers. obs.) so that many young are fledging as fruit is becoming particularly abundant.

METHODS

Birds were sampled during the dry (June, July) and wet (December, January) seasons 1994 and during the dry season (July, August) 1996. We used mist nets $(12 \times 2.6 \text{ m}, 36 \text{ mm mesh})$ set along narrow trails to sample birds; nets (10 to 20/day) were 30 to 50 m apart. The number of nets operated varied because of logistical constraints and the desire to prevent birds from remaining in nets for more than 1 h. Nets generally were opened close to dawn and kept open for 6 to 7 hs/day, depending on weather (rain, wind). Captured birds were identified, weighed, and banded with a numbered aluminum leg band. Each bird was held in a plastic container for approximately 5 min to collect fecal samples. Birds were processed and released at the capture site. Birds were assigned to migratory guilds based on literature accounts (Hilty & Brown 1986, Isler & Isler 1987, Narosky & Yzurieta 1993, Curson et al. 1994, Stotz et al. 1996,) and personal observations.

Mist nets are a valuable tool for sampling birds (Stotz et al. 1996) but their use is somewhat controversial (see Remsen & Good [1996] for a recent review). As in previous papers (e.g., Blake & Loiselle 1991, Loiselle & Blake 1991), we use capture rates (i.e., numbers of birds captured per 100 mist net hours [1 mist net open 1 hour = 1 mist net hour]) as an index of the activity of birds in the understory without making claims about abundance per se. We do use changes in capture rates between seasons as an indication of changes in activity and suggest that in many cases (e.g., for migrants) these changes in capture rates do reflect changes in abundance; in other cases, changes in capture rates likely reflect changes in behavior (i.e., birds shifting foraging height from understory to canopy in concert with changes in season).

Fecal samples from 1994 were analyzed by separating fruits from arthropods (1996 samples are not yet analyzed). Fruit species were identified (when possible) using a reference collection of seeds from the area and insects were identified (when possible) to order. All samples were retained so that unidentified fruit seeds can be identified later as the reference collection increases. For each bird species, we recorded the total number of times each item (e.g., Coleoptera, Diptera, Myrtaceae seeds, etc.) appeared in fecal samples as well as the number of fecal samples that contained only insects, only fruit seeds or pulp, or a combination of insects and fruit.

Sampling effort (number of nets) varied among sites and seasons so we expressed results in terms of capture rates. We compared capture rates between seasons within forest, between forests within season, and between years for dry season samples. Because samples were collected from single sites at each elevation, results of statistical tests must be considered primarily descriptive and valid only for the sites being compared. We used Fisher's Exact test for species represented by at least 6 captures (combined total for both seasons or sites being compared) and Chi² tests for total captures. Comparisons were based on actual numbers (not rates) with expected values based on number of net hours. Because samples differed in total numbers of captures, we could not directly compare number of species between samples (i.e., elevations, seasons). Instead, we compared species richness (number of species) between samples using rarefaction techniques based on a null model simulation (Ecosim V.1.0, Gotelli & Entsminger 1997). Rarefaction is a useful technique when sample sizes differ (i.e., numbers of individuals; see Gotelli & Graves 1996).

RESULTS

Community composition. We captured a total of 660 birds (359 in Selva Basal-SB hereafter; 301 in Selva de Mirtaceas-SM hereafter) representing 42 species (38 in SB; 31 in SM) and 14 families (counting subfamilies of Emberizidae separately) (Table 1); 8 species were captured only in SB and 3 only in SM. Recaptures accounted for only 3.6 % of the totals (12 in each site) and are not considered further. Most samples tended to be dominated by relatively few species; three to five species in each sample accounted for over 50 % of captures (Table 1). Species represented by only 1 or 2 captures accounted for at least 50 % of all species captured except during dry season 1994 in Selva de Mirtaceas when such species only accounted for 25% of the total. Particularly common species in the dry season included Syndactyla rufosuperciliata, Phylloscartes ventralis, Basileuterus bivitattus, and Atlapetes torquatus in SB and Basileuterus signatus, Atlapetes torquatus, and Chlorospingus opthalmicus (1994 only) in SM. During the wet season, Syndactyla rufosuperciliata, Lathrotriccus euleri, Turdus nigriceps, Atlapetes torquatus, and Thlypopsis sordida were common in SB whereas Elaenia strepera and Turdus nigriceps dominated captures in SM.

Number of species per sample ranged from 17 to 27 but differences were largely due to difference in number of captures. When all samples were compared based on 59 captures (the lowest total, from dry season 1996 in SM), mean species richness (based on 1000 simulations for each sample) ranged from 17.5 to 20.4. Species richness (based on rarefaction to 128 captures) for SB wet (mean of 1000 simulations = 23.7 [21.8— 25.6]) was, however, slightly less than during the dry season 1994 (27 species; see Table 1).

Capture rates. Considerable variation in capture rates was noted between wet and dry seasons in SB, between dry seasons in SM, and between SB and SM during dry seasons (Table 2). Capture rates (birds captured/100 mist net hours) were lowest during dry season 1996 in SM but highest during dry season 1994 in the same site. Capture rates at lower elevations did not change between years.

Marked changes in capture rates between seasons also were noted for several individual species (Table 2), particularly latitudinal and altitudinal migrants. In SB, several species rarely or never captured in dry season were captured more frequently in wet season (e.g., Elaenia strepera, Lathrotriccus euleri, Turdus nigriceps, Thlypopsis sordida). Comparable changes also were noted in SM, especially for Elaenia strepera, Turdus nigriceps, and Thraupis sayaca. Other species, in contrast, were captured less often during the wet season (SB: Basileuterus bivittatus, Chlorospingus opthalmicus; SM: Eriocnemis glaucopoides, Mecocerculus leucophrys, Phylloscartes ventralis, Basileuterus signatus, Chlorospingus opthalmicus); many of these species are not latitudinal migrants and changes in capture rates likely reflect changes in behavior, habitat shifts within an elevation, or altitudinal movements. Reciprocal changes between seasons at the two elevations (i.e., decreasing during the wet season at SM while increasing at SB) may indicate altitudinal shifts in distribution (e.g., Atlapetes torquatus).

Several species showed marked differences in capture rates between elevations. Particularly notable were Eriocnemis glaucopoides, Elaenia strepera, Mecocerculus leucophrys, Lathrotriccus euleri, Turdus nigriceps, Basileuterus bivittatus, B. signatus, and Thlypopsis sordida. Differences between elevations were most pronounced during wet season 1994 and dry season 1996. *Diets.* We obtained 226 fecal samples during 1994 (from 43 % of captures), representing 29 of the 42 species captured (Tables 3, 4). Number of different items recorded in each fecal sample varied; approximately 70 % contained one or two diffe-

rent items, 19 % three items, and about 11 % four or five items.

There were substantial differences between wet and dry seasons in number of fecal samples containing fruit seeds or pulp. Fecal samples were

| TABLE 1. Number of captures in Selva Basal and Selva de Mirtaceas during dry (1994, 1996) and wet (1994 |) |
|---|---|
| seasons in El Rey National Park, Argentina. Scientific names follow Stotz et al. (1996). | · |

| | | | Selva Basal | | Sel | va de Mirta | ceas |
|------------------------------------|-------|-----------------------------|-------------|--------|------------------|-------------|--------|
| | Ma | DRY 94 | WET 94 | DRY 96 | DRY 94 | WET 94 | DRY 96 |
| Micrastur ruficollis | | 1 | | | | | |
| Amazilia chinogaster | | 1 | 1 | 2 | 2 | | 1 |
| Friocnemis glaucopoides | | 1 | | | 8 | | |
| Sappho sparganura | | 1 | | 1 | 2 8 2 | 2 | |
| licumnus cirratus | | | 1 | | | | |
| Zeniliornis frontalis | | 1 | (# | | | | |
| ittasomus griseicapillus | | 2 | 1 | 2 | | | |
| iynallaxis azarae | | 4 | 1 | 2 | 5 | 2 | 1 |
| ynallaxis frontalis | I. | 0.5540 | 1 | | 1.040 | | |
| yndactyla rufosuperciliata | 122 | 10 | 15 | 10 | 5 | 8 | 5 |
| Satara cinerea | | | | 1 | 5 3 3 | | 1 |
| Todirostrum plumbeiceps | | 2 | | 1 1 | 3 | ¥ . | î |
| Phyllomyias sclateri | | 2 | | · · · | | | · · · |
| Elaenia strepera | L | 1.1 | 9 | | | 14 | |
| Mecocerculus lencophrys | A? | | | | 8 | 14 | 1 |
| Phylloscartes ventralis | A? | 9 | 3 | 14 | 6 | | à |
| | A? | 130 | 3 | 14 | 0 | | |
| Tolmomyias sulphurescens | AT. | | 3 | | | 1.12 | |
| ^p yrrhomyias cinnamomea | | | | | | 1 | |
| athrotriceus euleri | L | 20 | 22 | 1. | | 5 | |
| Snipolegus signatus | | 1 | | | | | |
| Troglodytes aedon | | | 14 | | | | 42 |
| Troglodytes solstitialis | | 2 | 2 | | 2 5 2 6 | 3 | 1 |
| Catharus dryas | | | 1 | | 2 | 3 | 4 |
| Turdus nigriceps | L. | 6 | 14 | 3 | 6 | 29 | 1 |
| Turdus rufiventris | A?. | 7 | 2 | 7 4 | 6 | 1 | 1 |
| Poospiza erythrophrys | | 2 | | 4 | 5 | 2 | 2 |
| Sporophila lineola | L | 7 2 1 2 2 19 | | | | | |
| Arremon flavirostris | | 2 | 4 | 2 | the second | | |
| Atlapetes citrinellus | | 2 | | 1 | 5 | 5 | 2 |
| Atlapetes torquatus | A? | 19 | 24 | 8 | 15 | 6 | 14 |
| Pheneticus aureoventris | L | 1 | 10.8 | 1.0 | | 0.0 | |
| Passerina brissoni | | 7 | | 1 | | | 1 |
| Chlorospingus ophthalmicus | A? | 11 | 3 | 3 | 23 | 2 | 1 |
| Thlypopsis sordida | A | | 21 | | | 2 2 6 | |
| Thraupis sayaca | L | | 3 | | | 6 | |
| Pipraeidea melanota | A? | 3 | 7 | | | 1 | |
| Diglossa haritula | 8.774 | 1.12 | 2 | | 2 | | |
| Wvioborus brunniceps | | 5 | 2 | | 2 | - 1 | 2 |
| Basileuterus bivittatus | | 23 | 6 | 12 | 6 | | - |
| Basileuterus signatus | | 2 | 5 | 1 | 18 | 5 | 10 |
| Cyclarhis gujanensis | | - | 2 | 2 | 10 | 1 | 1 |
| Vireo olivaceus | L | | 2 | ÷ | | | |
| Total species | | 27 | 25 | 20 | 23 | 22 | 19 |
| Total captures | | 128 | 152 | 79 | 141 | 101 | 59 |
| Total mist net hours | | 287 | 238 | 161 | 157 | 140 | 200 |

^a Migrant codes: A – altitudinal migrant, A? – possible altitudinal migrant, L – latitudinal migrant (at least partially).

TABLE 2. Results of Fisher's exact tests for differences in captures between seasons (D-W – dry vs. wet seasons 1994; D-D – dry 1994 vs. dry 1996) within a forest and within seasons (D94 – dry 1994; D96 – dry 1996; W94 – wet 1994) between forests. Species were tested if there was a total of a least 6 captures in the two sites (seasons) being compared (see Table 1). Total captures were compared using Chi² tests. ns=not significant; *=P<0.05; **=P<0.05; ***=P<0.01; **=P<0.001.

| Taxa | Selva | Basal | | ra de caceas | | elva Basal e Mirtace | |
|-----------------------------|-------|-------|---------|-----------------|-----------|-------------------------|----------|
| | D-W | D-D | D-W | D-D | D94 | W94 | D96 |
| Eriocnemis glaucopoides | ••••• | 1 | *** | | 冷冷冷 | | |
| Synallaxis azarae | | | ns | ns | ns | | |
| Syndactyla rufosuperciliata | ns | | ns | ns | ns | ns | * |
| Elaenia strepera | *** | | 特特特特 | | | ** | |
| Mecocerculus leucophrys | | | 外处 | 가가 | 传传传传 | | |
| Phylloscartes ventralis | | | 가 가 | ns | ns | | * |
| Lathrotriccus euleri | | | | | | * * | |
| Troglodytes solstitialis | | | ns | ns | * | | |
| Catharus dryas | | | | ns | | | |
| Turdus nigriceps | ** | ns | **** | * | ns | **** | |
| Turdus rufiventris | ns | ns | ns | * | ns | | 20-20- |
| Poospiza erythrophrys | | ns | ns | ns | * | | ns |
| Atlapetes citrinellus | | | ns | ns | ** | | |
| Atlapetes torquatus | * | | * | ns | ns | ** | ns |
| Passerina brissoni | 가가 | | | | 20- | | |
| Chlorospingus opthalmicus | 가 | | * * * * | 26-26-26-26 | *** | | |
| Thlypopsis sordida | *** | | | | | 20-20-20- | |
| Thraupis sayaca | | | 外外 | | | ns | |
| Pipraeidea melanota | ns | 1 | | | | ns | |
| Myioborus brunniceps | ns | | | | ns | | |
| Basileuterus bivittatus | *** | ns | 가가 | ** | 20- | ns | 计外传令 |
| Basileuterus signatus | ns | | ** | 铃铃 | 가가가가 - | ns | 과과 |
| Total species tested | 14 | 10 | 16 | 14 | 16 | 10 | 7 |
| Total captures | *** | ns | * | 가가가가 | *** | ns | 26-26-26 |

dominated by insect remains during the dry season: 51 of 55 samples in SB and 29 of 36 samples from SM contained only insect parts (Chi² comparisons for equal distribution between insects only and samples with fruit = 40.2 and 13.4 for SB and SM, respectively; P<0.001 in both cases). In contrast, fruit samples were much more common during the wet season, particularly in SM: 39 of 78 samples from SB and 42 of 57 samples from SM contained fruit or fruit and insects (Chi² = 0 for SB; Chi² = 12.8, P < 0.001 for SM). Samples from Turdus nigriceps accounted for 20 of the samples with fruit in SM; with this species excluded there was no difference in number of samples with insects only (15) or with fruit (22) (Chi² = 1.3). Seasonal patterns (dry vs wet season) in relative proportions of samples with insects or

with fruit differed in both SB (Chi² = 26.0) and SM (Chi² = 26.0, P<0.001, both cases). Overall patterns did not differ between forests during the dry season (Chi² = 3.0, P<0.10) but did in the wet season (Chi² = 7.7, P<0.01); differences in the wet season were not pronounced between forests when *Turdus nigriceps* was omitted from the comparison (Chi² = 2.7, P<0.10).

Species differed considerably in use of fruit. Among the most frugivorous were *Elaenia strepera* (100 % of samples with fruit), *Thraupis sayaca* (100 %), *Turdus nigriceps* (65 %), and *Thlypopsis sordida* (60 %). A total of 15 species consumed fruit whereas almost all species were recorded with insect parts in fecal samples (except *Passerina brissoni* — only one fecal sample, containing only pulp). Several species present in the area TABLE 3. Number of fecal samples containing only insect parts (I), only fruit seeds or pulp (F), or a combination of insects and fruit (IF) collected during dry and wet seasons, 1994, from birds captured at two elevations in El Rey National Park, Argentina.

| | | | Selva | Basal | | | <u></u> | Se | lva de l | Mirtace | 215 | |
|-----------------------------|-----|-----|-------|-------|-----|------|---------|-----|----------|---------|-----|-----|
| Taxa | | Dry | | | Wet | | | Dry | | | Wet | |
| | I | F | IF | 1 | F | IF | I | F | IF | 1 | F | IF |
| Synallaxis azarae | 1 | | | | | | 1 | | | | | |
| Syndactyla rufosuperciliata | 5 | | 1 | 5 | | 1 | 1 | | | 4 | | 1 |
| Todirostrum plumbeiceps | | | | | | | 1 | | | | | |
| Phyllomyias sclateri | 1 | | | | | | 1 | | | 1 | | |
| Elaenia strepera | | | | | 3 | | | | | | 6 | 1 |
| Mecocerculus leucophrys | | | | | | | 4 | | | | | |
| Phylloscartes ventralis | - 3 | | | 1 | | | 1 | | | | | |
| Tolmomyias sulphurescens | | | | 2 | | | | | | | | |
| Pyerboniyias cinnamomea | | | | | | | | | | 1 | | |
| Lathrotriccus euleri | | | | - 5 | | - 30 | | | | 2 | | |
| Knipolegus signatus | 1 | | | | | | | | | | | |
| Troglodytes solstitialis | 2 | | | 2 | | | | | | 2 | | |
| Catharus dryas | | | | 1 | | | -1 | | | 11152 | | |
| Turdus nigriceps | 2 | | 1 | | 8 | 2 | 3 | | 1 | | 16 | 4 |
| Turdus rufiventris | 4 | | 1 | 1 | 1 | 1 | 1 | | | | 1 | |
| Poospiza erytbrophrys | 100 | | 1.10 | 112 | | | 2 | | 1 | | | -1 |
| Arremon flavirostris | 1 | | | | | | | | | | | |
| Atlapetes citrinellus | 1 | | | | | | | 1 | 1 | 1 | | 1 |
| Atlapetes torquatus | 7 | | | 7 | | 6 | 2 | | 1 | | 2 | 1 |
| Passerina brissonii | | 1 | | | | | | | | | | |
| Chlorospingus ophthalmicus | 4 | | | 1 | | | 3 | | 2 | | | - 1 |
| Thlypopsis sordida | 1.0 | | | 6 | | 8 | 1 | | | | | 1 |
| Thraupis sayaca | | | | | 1 | 1 | | | | | | 4 |
| Pipraeidea melanonota | 2 | | | 2 | | 2 | | | | | | 1 |
| Myioborus brunniceps | 4 | | | 2 | | | 1 | | | | | 1.1 |
| Basileuterus bivittatus | 14 | | | 2 1 1 | | 2 | 3 | | | | | |
| Basileuterus signatus | 1 | | | 1 | 1 | | 5 | | | 3 | | 1 |
| Cyclarhis gujanensis | 16 | 1 | | 1 | | | | | | 1 | | 1.0 |
| Vireo olivacens | | | | 1 | | | | | | | | |
| Total number of samples | 51 | 1 | 3 | 39 | 13 | 26 | 29 | 1 | 6 | 15 | 25 | 17 |

during both dry and wet seasons increased their use of fruit during the wet season (based on proportional occurrence of fecal sample with fruit) (e.g., *Turdus nigriceps, Atlapetes torquatus*). Increased use of fruit corresponded with greater availability and diversity of fruits (pers. obs.).

DISCUSSION

Bird communities in montane forests of northwestern Argentina exhibit considerable variation in species composition and relative abundance (capture rates) both between and within elevations. Although the observed patterns are in general agreement with other studies (Vides 1992), it is important to emphasize that the observed patterns and their interpretation are based on a limited data set. Consequently, several different explanations are possible for the observed variation. Variation in capture rates and species composition may, for example, be related to site specific effects or sampling error. We sampled only one area at each elevation so it is possible that the results obtained apply only to those sites and are not representative of forests at those elevations in general. However, given that vegetation present in the sampled areas was similar to that present at other areas at the same elevation in the park (Brown 1986; pers. obs.), it is likely that the results are representative of the forest as a whole. Sampling error is more likley to be a problem for individual species (e.g., *Chlorospin*gus opthalmicus) than for overall community patterns. Variation in capture rates of individual species may reflect changes in behavior (flocking vs. territorial; canopy vs. understory foraging) that are not revealed by mist net captures.

Capture rates also are influenced by arrival and departure of latitudinal migrants and seasonal shifts along the elevational gradient by resident species (altitudinal migration), patterns also observed in bird communities in montane forests of Central America (Stiles 1985, Stiles & Clark 1989, Loiselle & Blake 1991). Variation in abundance of resources, including insects, fruit, and nectar, influences dynamics of bird communities in many temperate and tropical regions (Blake & Hoppes 1986, Wiens 1989, Blake & Loiselle 1991, Loiselle & Blake 1991, Levey & Stiles 1992, Poulin et al. 1992, Lefebvre & Poulin 1996) and likely is an important influence on bird communities in El Rey National Park as well. Nectarivores (e.g., Sappho sparganura, Eriocnemis glaucopoides) were more frequently encountered during the dry season, when flower abundance and, presumably, nectar availability is higher (pers. obs.) whereas several species of frugivores were captured much more frequently during the wet season, during the period of peak fruit production. Similarly, arrival of latitudinal migrants for breeding is coincident with production of fruit, which many species use as a major part of their diet. Overall, there was a substantial increase both in the number of species eating fruit and the proportion of individuals within a species eating fruit during the summer (wet season), the period when fruit is most abundant.

Among the more common latitudinal migrants were *Elaenia strepera, Lathrotriccus euleri*, and *Turdus nigriceps*. Captures rates of species differed between elevations, suggesting differences in habitat preferences. In some cases (e.g., *Elaenia, Turdus*), differences between seasons and elevations may be related to differences in availability of fruit resources. Production of fruit by members of the Mirtaceae peak during the wet season when breeding is occurring and migrants are present. Similarly, Selva de Mirtaceas is dominated by members of that family; trees produce abundant crops of fruits that are consumed by birds. In other cases (e.g., *Lathrotriccus*), differences between elevations are not likely due to differences in fruit resources as no evidence of fruit consumption was found. Birds may be responding to differences in insect numbers (often higher in wet seasons) but we have no information on insect abundance with which to evaluate this possibility.

Seasonal shifts along the elevational gradient likely are an important component of the dynamics of communities in this area. Vides (1992) suggested that as much as 50 % of the species in montane forests in northwestern Argentina (at a site near Tucumán) may exhibit regular altitudinal shifts in distribution. Although our data are preliminary and need further confirmation, it appears that this type of movement occurs in a number of species in El Rey and helps account for differences in bird communities between elevations. Capture rates of Atlapetes torquatus, for example, declined in Selva Mirtaceas coincident with higher capture rates in Selva Basal. Although the distances traveled are not great, the shift in elevation (from 1300 to 900 m) may nonetheless be important. In Costa Rica, shifts of 200 m between seasons are exhibited by a number of species, particularly members of the Pipridae (Loiselle & Blake 1991, unpubl. data). Similarly, Thlypopsis sordida is known to shift along elevational gradients (Isler & Isler 1987) and the higher capture rates during the wet season in Selva Basal may be at least partially in response to increases in fruit resources.

Altitudinal shifts may be in response to changes in resources, as has been demonstrated elsewhere but also may be in response to seasonal changes in environmental conditions (see Ramos 1983). Higher elevations in the park are more likely to experience colder conditions during winter, with frost and snow a greater possibility. The winter of 1996 was especially severe, with considerable snow recorded in Selva de Mirtaceas forest (H. Grau, pers. comm.). This severe weather may be one explanation for the much lower capture rates in that forest compared to winter 1994. Clearly, samples from additional years and seasons are needed to evaluate the effects of such weather conditions. TABLE 4. Number of times different insect or fruit types were recorded in fecal samples from birds captured in El Rey National Park, Argentina. Data are combined results of samples collected during the dry and wet seasons of 1994.

| | | Bl | Col | Dip | Eg | For | Hem | Hym | Lar | Mol | Thy | Ni. | Myr | Sol | Nif | Fs | Item |
|-----------------------------|-----|----|----------------|-----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Swnallaxis azarae | | | | - | | | | | L | | | 7 | | | | 7 | 4 |
| Syndactyla rufosuperciliata | 12 | | 11 | 4 | | 6 | | ŝ | 7 | | | ŝ | | 7 | | 1 | 7 |
| Todirostrum plumbeiceps | - | | | 1 | | | | | | | | | | | | - | 7 |
| Phyllomvias sclateri | | | 7 | | | | | | | | | | | | | 7 | 5 |
| Flaenia strebera | | | | | | 1 | | | | | | | | | | 10 | 15 |
| Mecocerculus leucophros | | | 2 | 2 | | 1 | | | | | | | | | | 4 | 80 |
| Phylloscartes mentralis | | | 1 (* | | | 0 | | | | | | | | | | 3 | 9 |
| Tolmonnia collebracióne | | | , c | • | | I | | 6 | | | | | | | | 2 | 4 |
| ounomistas supparescens | | | 1 - | | | | | · - | | | | | | | | 1 | 7 |
| I atherations and an | " | | • £ | | | ſ | | 5 | | | | 1 | | | 7 | 10 | 26 |
| Knihologus signatus | r | | 2 | | | 1 | | • | | | | 1 | | | | 1 | 1 |
| Troolodytes solstitialis | 4 | | | 2 | | ŝ | | | | | | 7 | | | | 6 | 16 |
| Cathanus dimine | • | | | I | | 2 | | | | | | | | | | 2 | 2 |
| Turdas minustas | " | | 4 | | | | | | 4 | | | 9 | 12 | 6 | 13 | 37 | 56 |
| Turdus rufinentris | . 0 | | 4 | | | ŝ | | 1 | 1 | | | 1 | | 1 | ŝ | 10 | 19 |
| Poostiza eruthrothrus | 0 | | - | | | 1 | | 1 | 7 | | | | | | 7 | 4 | 6 |
| Arremon flaminstris | I | | · - | | | 1 | | | | | | | | | | 1 | 7 |
| Atlatetes citrinellus | | | - | | | - | | | | | | 4 | | | ŝ | 5 | 6 |
| Atlanetes tornuatus | 6 | | 12 | | | 12 | | 7 | | | | œ | | 8 | 3 | 26 | 49 |
| Passering brissonii | 1 | | | | | | | | | | | | | | - | 1 | 1 |
| Chlorospinous ophthalmicus | 9 | | ę | ŝ | | 9 | - | 7 | _ | | | 1 | | 1 | £ | 11 | 27 |
| Thymothesis sordida | 4 | | 12 | | | 9 | £ | ~ | | | | 7 | | 8 | 1 | 15 | 43 |
| Thraupis savaca | 6 | | ŝ | | | 7 | | £ | | | | | 2 | 4 | 7 | 9 | 8 |
| Pipraeidea melanonota | ę | | | | | 7 | | 1 | 7 | | | 7 | | 7 | ŝ | ~ | 15 |
| Myioborus brunniceps | ŝ | | ŝ | | | 7 | | ŝ | | | | - | | | | ~ | 12 |
| Basileuterus bivittatus | ŝ | | ~ | | | œ | | ĉ | 7 | | ~-1 | Ś | | | 7 | 20 | 39 |
| Basileuterus signatus | 4 | | ~ | | | 9 | | ŝ | | | | 7 | | | - | 11 | 25 |
| Cvclarhis quianensis | 1 | | 7 | | | | | | | | | | | | | 7 | 4 |
| Vireo olivaceus | | | 1 | | | | | | | | | | | | | | 7 |
| Total number of samples | 58 | 3 | 100 | 25 | - | 78 | 7 | 39 | 14 | 1 | 1 | 41 | 19 | 44 | 64 | 226 | |

Results of this study indicate that bird communities in montane forests of northwestern Argentina display considerable spatial and temporal variation in both composition and abundance. There are a number of possible causes for this variation, with different factors likely to be important for different species. A more complete understanding of these patterns requires additional study.

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REFERENCES

- Bianchi, A. 1981. Las precipitaciones en el noroeste argentino. INTA.
- Blake, J. G., & W. G. Hoppes. 1986. Resource abundance and microhabitat use by birds in an isolated east-central Illinois woodlot. Auk 103: 328–340.
- Blake, J. G., & B. A. Loiselle. 1991. Variation in resource abundance affects capture rates in birds of three lowland habitats in Costa Rica. Auk 108: 328–340.
- Brown, A. D. 1986. Autoecology de Bromeliaceas epifitas y su vinculacion con *Cebus apella* (Primates) en el noroeste Argentino. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
- Brown, A. D., & E. D. Ramadori. 1989. Patron de distribucion, diversidad y caracteristicas ecologicas de especies arboreas de las selvas y bosques montanos del noroeste de Argentina. Anales VI Congreso Forestal Argentino: 177–181.
- Chalukian, S. C. 1991. Regeneracion, sucesion y plantas invasoras en un bosque de Yungas, Salta, Argentina. Ms. Thesis. Programa Regional en Manejo de Vida Silvestre para Mesoamerica y el Caribe.
- Chesser, R. T. 1994. Migration in South America: an overview of the austral system. Bird Conserv. Intl. 4: 91–107.
- Curson, J., Quinn, D., & D. Beadle. 1994. Warblers of the Americas: an identification guide. Boston.

- Gotelli, N. J., & G. L. Entsminger. 1997. EcoSim. Null models software for ecology. Version 1.0. Kesey-Bear, Inc.
- Gotelli, N. J., & G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D. C.
- Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton.
- Isler, M. L., & P. R. Isler. 1987. The tanagers: natural history, distribution, and identification. Washington D. C.
- Lefebvre, G., & B. Poulin, B. 1996. Seasonal abundance of migrant birds and food resources in Panamanian mangrove forests. Wilson Bull. 108: 748–759.
- Levey, D. J., & F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. Amer. Nat. 140: 447–476.
- Loiselle, B. A., & J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72: 180–193.
- Marantz, C. A., & J. V. Remsen. 1991. Seasonal distribution of the Slaty Elaenia, a little-known austral migrant of South America. J. Field Ornithol. 62: 162–172.
- Narosky, T., & D. Yzurieta. 1993. Birds of Argentina and Uruguay: A field guide. Buenos Aires.
- Poulin, B., Lefebvre, G., & R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295– 2309.
- Ramos, M. A. 1983. Seasonal movements of bird populations at a Neotropical study site in sourthern Veracruz. Ph. D. diss., University Minnesota, St. Paul.
- Remsen, J. V., Jr., & D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 381–398.
- Stiles, F. G. 1985. On the role of birds in the dynamics of Neotropical forests. Pp. 49–59 *in* Diamond, A. W., & T. Lovejoy (eds.). Conservation of tropical forest birds. Cambridge, U. K.
- Stiles, F. G., & D. A. Clark. 1989. Conservation of tropical rain forest birds: a case study from Costa Rica. American Birds 43: 420–428.
- Stotz, D. F., Fitzpatrick, J. W., Parker, T. A., III, & D. K. Moskovitz. 1996. Neotropical birds: ecology and conservation. Chicago.
- Wiens, J. A. 1989. The ecology of bird communities. Cambridge.
- Vides, R. 1992. Estudio comparativo de las taxocenosis de aves de los bosques montanos de la Sierra de San Javier, Tucumán: Bases para su manejo y conservacion. Tesis Doctoral. Fac. de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina.