ORNITOLOGIA NEOTROPICAL

Volume 19

2008

No. 1

ORNITOLOGIA NEOTROPICAL 19: 1–14, 2008 © The Neotropical Ornithological Society

A COMPARISON OF GALLERY AND DRY FOREST AVIAN COMMUNITIES IN THE GRAN CHACO OF BOLIVIA

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Resumen. - Una comparación de las comunidades de aves de bosque de galería y bosque seco en el Gran Chaco de Bolivia. - Realizamos un estudio sobre la comunidad de aves en un sitio en el Gran Chaco de Bolivia, compuesto principalmente por un bosque de galería sobre el borde del Río Parapetí, en un paisaje de bosque seco espinoso. Presentamos el primer análisis detallado de la diversidad de aves entre épocas y hábitats en el chaco de Bolivia, utilizando datos de observaciones y de captura. De las 101 especies detectadas en bosque seco y bosque de galería en el sitio, 20% fueron registradas exclusivamente en el bosque seco y 20% fueron registradas exclusivamente en el bosque de galería; 60% fueron registradas en los dos hábitats. Un análisis de las asociaciones de hábitat a nivel continental con su asociación de hábitat a nivel local demostró que especies que son mas típicas de bosque siempre verde, cual no es un hábitat en el chaco, tienden a ser encontradas en el bosque de galería en el sitio, mientras que especies asociadas con bosque deciduo tropical (hábitat típico del chaco boliviano) son mas típicas del bosque seco en el sitio de estudio. Examinamos las asociaciones de hábitat de las especies en más detalle usando redes de neblina. El bosque de galería fue significativamente más rico y diverso en especies capturadas que el bosque seco. Cuando las asociaciones de hábitat fueron comparadas entre épocas de lluvia y seca, el bosque seco en la época seca demostró la más baja riqueza y diversidad que cualquier otra combinación de época y hábitat. En general, los resultados indican que diferencias entre hábitats en esta región del Gran Chaco es un factor determinante en la diversidad local de la avifauna.

Abstract. – We studied the bird community at a site in the Gran Chaco of Bolivia composed principally of gallery forest bordering the Parapetí River within a larger landscape of dry thorn forest. We present the

first detailed analysis of local avian community diversity across seasons and habitats for the bolivian chaco, utilizing both observational and mist-net capture data. Of the 101 species recorded in dry and gallery forest, 20% were recorded exclusively in gallery forest and 20% were recorded exclusively in dry forest; 60% were recorded in both habitats. Analysis of species habitat affinities at the continental scale relative to their habitat occupancy at the study site revealed that species typical of lowland evergreen forest, which is not a chaco habitat, tend to be found in gallery forest at the site, while species associated with tropical deciduous forest/arid lowland scrub (habitats typical of the bolivian chaco) are more likely to be found in the dry forest at the site. We examined species-habitat associations in more detail through mist-netting. Richness and diversity as measured by mist-netting were significantly higher in gallery forest than dry forest. When habitat associations were compared across wet and dry seasons, the dry forest in the dry season exhibited the lowest levels of species richness and diversity of any season-habitat combination. Overall, our results suggest that habitat differences in this region of the Gran Chaco play an important role in maintaining local avian community diversity. *Accepted 20 September 2007*.

Key words: Diversity, habitat associations, Kaa-Iya National Park, Parapetí River, rarefaction, seasonality.

INTRODUCTION

South America's Gran Chaco is a vast forest, woodland and grassland complex of over 1,000,000 km² shared primarily by Argentina, Bolivia and Paraguay. The Gran Chaco represents the largest dry forest system in South America and the second largest forested area on the continent after the Amazon rainforest (The Nature Conservancy *et al.* 2005). Yet, in spite of its importance as a major Neotropical ecoregion, the chacoan avifauna remains relatively understudied, especially at the local scale where patterns of habitat associations remain poorly known for many of the region's 500 bird species (Kratter *et al.* 1993).

Studies from other dry ecosystems suggest that riparian habitat can play a significant role in shaping local avian community composition. For example, riparian habitat in Queensland, Australia, was found to hold higher bird species richness than surrounding dry habitat (Bentley & Catterall 1997). Woinarsky *et al.* (2000) found higher species richness in riparian forest than in the surrounding savannah habitat in Northern Territory, Australia, with the greatest differences in species composition between riparian and non-riparian habitats occurring in areas of lower rainfall. In southern Africa, Simmons & Allan (2002) detected higher bird species richness in riparian habitat bordering the Orange River than in the surrounding dry habitat matrix.

In the Neotropics, riparian habitat regularly occurs in a variety of dry forest ecosystems; however, few studies exist of the impact of riparian habitats on local bird community composition in such dry forests. Silva (1995) proposed that gallery forest may have had a major role in structuring the current bird species composition of the cerrado ecoregion in Brazil, estimating that upwards of 30% of species that breed in the cerrado may have expanded their ranges from Amazonian or Atlantic Forests by following gallery forests into the cerrado. Likewise, in the chaco of Argentina, Nores (1992) documented the presence of several bird species more typical of Paranaense humid forest east of the chaco that had presumably extended their ranges along gallery forests into the chaco.

The Parapetí River, the major watercourse in the bolivian chaco, supports a distinct gallery forest corridor within the drier thorn forest matrix that characterizes the region. In an extensive review of available data for bird species distributions across forest types in the bolivian chaco, Guerrero & Arambiza (2001) found evidence for habitat specificity of several species in the gallery forest along the Parapetí River, as well as in several other chaco habitat types across the region. Likewise, Parker *et al.* (1993) documented differences in bird community composition between habitats in the bolivian chaco, while Kratter *et al.* (1993) found a distinct bird community in low, open scrub vegetation relative to that of a primarily woodland chaco site. They attributed the species turnover among these and other sites they sampled as related to moisture gradients and vegetation stature.

In order to evaluate such patterns at a local, population-level scale, we studied bird community composition over a seven-year period (1998-2005) at a site in the bolivian chaco comprised of gallery forest along the Parapetí River and dry thorn forest away from the river. Because of the diverse lines of research on birds at the study site, including bird banding (Jahn et al. 2002a, 2002b), censusing and taxonomic surveys (Porzecanski 2003, Dobbs & Huizinga 2005) and studies on plant-animal interactions (Levey et al. 2006), a large body of information has been compiled on the local bird community from 1998 to 2005, making this one of the beststudied sites in terms of local avifauna composition in the northern chaco. The objectives of this study were to: 1) Characterize the richness, diversity and seasonality of local bird communities in gallery and dry forest habitats, 2) Relate habitat associations of species to their habitat affinities at the continental scale, and 3) Evaluate the results relative to similar studies from other ecosystems and their potential for informing conservation planning.

STUDY SITE AND METHODS

Data were collected at Estancia San Julián, Department of Santa Cruz, Bolivia (19°47'S, 62°42'W), approximately 500 m a.s.l. The site is characterized by extreme contrast between dry and wet seasons, with monthly precipita-

tion during the study period varying from 0 to 244 mm (R. Cuéllar unpub.). The two main habitats at the site are a semideciduous riparian forest ("Algarrobal freatófilo", sensu Navarro & Fuentes 1999) (hereafter "gallery forest") found along the Parapetí River (up to \sim 500 m. from the river) and a continuous semideciduous, dry thorn forest on sandy soil (hereafter "dry forest") which covers most of the area > 500m from the river. The river, which flows south to north across the western portion of the bolivian chaco, is seasonal with little to no ground water present at the study from approximately September to site December. Throughout the year, however, the water table within 1 km of the river is much shallower (~ 10 m deep) than it is far from the river (at 20 km away it can be > 100 m deep; A. Noss pers. com.) and the gallery forest is markedly less deciduous than the dry forest.

The dry forest is predominantly a formation of Ruprechtia, Acacia and Caesalpinia trees, with a canopy 4-8 m in height, and Cereus cacti. Emergent trees 15-20 m high are largely Aspidosperma quebracho-blanco, Schinopsis quebracho-colorado, Chorisia insignis and Ziziphus mistol. The gallery forest is comprised primarily of Bougainvillea, Senna and Sideroxylon trees with a canopy height of 4-6 m. Emergent tree species are mostly Schinopsis cornuta and Prosopis chilensis, 15-20 m in height. Bromelia serra is the dominant, non-woody ground level species in both habitats. Cattle were present in low densities in both forest types; nonetheless, the site was chosen because of the relatively conserved nature of the vegetation in relation to the surrounding area.

Visits to the study site were made on the following dates: 1) Mist-netting on 16 October–5 November 1998, 28 March–29 April 1999, 16 September–14 November 2000, and 24 February–15 May 2001 by Alex Jahn (AJ) and Ana Maria Saavedra (AS), 2) Specimen collecting by Ana Luz Porzecanski (AP) and Jacqueline Weicker (JW) on 30 October–14

November 2000, and 3) Daily observations on 7 March–26 May 2003 by Robert C. Dobbs (RCD), 3 March–30 April 2004 by R. Ian Horn (RIH) and AS, and 15–28 March 2005 by RCD and RIH.

Observations of birds were made by AJ, AS, RCD and RIH on all days listed above during daily walks around the study site as well as during operation of mist nets. Observations were made in 1998 and 1999 by AJ and AS while operating mist-nets in dry forest (45 observation days). From 2000 to 2005, observations were made while operating mist nets and during walks in gallery and dry forest (approx. 230 observation days). Observations were opportunistic (i.e., not standardized by time or area covered) and conducted in dry forest at the mist-nets as well as at other sites across the dry forest, nearer to the river and in areas where cattle densities and therefore impact on the understory was larger than at the nets such that quantitative comparisons herein are based upon data from mist-netting.

In order to quantify patterns across habitats more objectively, we conducted mist-netting and banding using standard methods (Ralph et al. 1993), employing one net array of 10-15 nets (12 m x 2.6 m, 35 mm mesh), each net separated by approximately 15 m, with one array in dry forest and one in gallery forest; the two arrays were separated by ~ 6 km. All birds captured were banded with a uniquely-numbered aluminum leg band of the Museo de Historia Natural Noel Kempff Mercado Bird Monitoring Program. We mistnetted birds in dry forest in the dry season of 1998 (14 days, 16 October-5 November) and 1999 (10 days, 13-23 October), and in the wet season of 1999 (21 days, 28 March-29 April). We mist-netted birds in gallery forest in the dry season of 2000 (41 days, 16 September-14 November) and the wet season of 2001 (52 days, 24 February-15 May). The same net lanes were used in each habitat across seasons, except in the wet season of 2001 when we opened five additional nets (for a total of 15 nets) in gallery forest. Nets were opened from 15 min before sunrise for 4 h each morning, due to elevated temperatures during the rest of the day. Nets were not opened during precipitation or during moderate to strong winds. We operated mist nets at the end of the dry season and from the middle to the end of the rainy season.

Comparisons between local habitats for species which are migratory or may have some migratory individuals (i.e., partial migrants) may result in patterns which are due to long-distance movements by these species. We therefore take a conservative approach in including species for analyses by not considering any species known to have migratory populations in South America. Thus, we do not consider here species listed as Nearctic-Neotropical migrants or austral migrants (including partial migrants) by Parker et al. (1996) in the present analyses. We do not attempt to classify which individuals were breeding at the site because, although the breeding condition of birds was checked during captures, presence of a brood patch or cloacal protuberance does not necessarily mean that the individual is breeding at the site or in the habitat it was captured. Furthermore, for analyses using observational data, such data is not available.

Because the number of net-hours was not equal between habitats, we calculated expected species richness and diversity by rarefaction using Ecosim 7.0, which computes expected species richness through Monte Carlo randomization (we used 1000 iterations) (Gotelli & Entsminger 2001), permitting comparisons between habitats based on the lowest number of individuals sampled. We also compared captures/net-h between habitats at the species level, using a minimum of 15 total captures per species (i.e., combining

Species	Ν	Mann- Whitney U	Р	Higher mean rank in
Large Antshrike (Taraba major)	15	1897.0	0.069	Gallery forest
Pearly-vented Tody-Tyrant (Hemitriccus margaritaceiventer)	21	2083.5	0.941	Gallery forest
Fuscous Flycatcher (Cnemotriccus fuscatus)	131	1781.5	0.133	Dry forest
Brown-crested Flycatcher (Myiarchus tyrannulus)	24	1993.0	0.440	Dry forest
Rufous-browed Peppershrike (Cyclarhis gujanensis)	18	1968.5	0.297	Gallery forest
Masked Yellowthroat (Geothlypis aequinoctialis)	15	1800.0	0.009	Gallery forest
Black-backed Grosbeak (Phencticus aureoventris)	35	1512.0	< 0.0001	Dry forest
Ultramarine Grosbeak (Cyanocompsa brissonii)	15	1822.5	0.012	Gallery forest
Dull-colored Grassquit (Tiaris obscura)	22	1781.0	0.013	Gallery forest
Red-crested Finch (Coryphospingus cucullatus)	159	1879.0	0.275	Gallery forest

TABLE 1. Comparison of captures/net-h between gallery and dry forest of common species (= 15 individuals/species captured in gallery and/or dry forest).

captures of both habitats) as a sample size limit for analysis (Table 1).

To explore habitat affinities at broader scales, we compared presence/absence of species in gallery and dry forest at the study site (using both observations and capture data) to the typical habitats of these species throughout the Neotropics. We used the habitat classification system of Parker et al. (1996) that assigns bird species to broad habitat categories. We focused on three habitat categories: "tropical lowland evergreen forest", which is coded F1 in Parker et al. (1996) (a habitat that does not occur in the chaco), "tropical deciduous forest" (F7), and "arid lowland scrub" (N1) (the latter two habitats are typical of the bolivian chaco). We split species into two groups, assigning a species to "tropical evergreen forest" when it was assigned to F1 by Parker et al. (1996) but not to F7 or N1 and classified a species as "deciduous forest/arid scrub" when classified by Parker et al. (1996) as associated with F7 or N1 but not with F1. Although Parker et al. (1996) have a "gallery forest" classification, we do not consider it here because our objective is to determine if the gallery forest at the study site is responsible for harboring species more typical of habitat not found in Bolivia's chaco (i.e., tropical evergreen forest).

RESULTS

We recorded 101 species (of which 54 were Passerines) through observations and mistnetting. We recorded 81 species in dry forest, of which 21 were found exclusively in that habitat. We recorded 80 species in gallery forest, with 20 exclusively found there. Sixty species (60% of the total) were found in both habitats.

There was an association between habitat affinities of species at the continental level and their habitat occupancy at the site: 25% of species exclusively recorded in gallery forest at the site are typical of tropical evergreen forest at a continental scale (Parker et al. 1996), while 5% of species recorded exclusively in gallery forest are typical of deciduous forest/arid scrub, though this is not a significant relationship ($\chi^2 = 2.67$, P = 0.102) (Fig. 1). Thirtyeight percent of species recorded exclusively in dry forest are typical of deciduous forest/ arid scrub at the continental level and 5% of species recorded exclusively in dry forest at the site are typical of tropical evergreen forest $(\chi^2 = 5.44, P = 0.020)$ (Fig. 1).



FIG. 1. Percent of species exclusively recorded in gallery or dry forest as a function of their habitat affinities at a continental scale; numbers above and in bars represent sample size.

Captures by habitat. We captured a total of 51 species, 40 of which were found in gallery forest and 28 in dry forest. There were significantly fewer species which were captured relative to those observed in dry forest ($\chi^2 =$ 7.72, P = 0.005), while in gallery forest there was no difference ($\chi^2 = 0.00$, P = 1.000). Species rarefaction curves for both habitats did not reach an asymptote, although that of gallery forest appeared to be nearing an asymptote (Fig. 2). Thus, mist-netting likely sampled the common species. Sixty-five percent (33 species) of species captured were Passerines.

Species richness of birds as measured by captures was significantly higher in gallery than in dry forest (i.e., 95% confidence intervals do not overlap; Fig. 3), while species diversity was slightly higher in gallery forest (Table 2). Overall, capture rates were similar between the two habitats, with 0.10 captures/ net-h (Table 1).

Of the species for which capture data were compared between habitats, 6 of the 10 showed no significant difference (at the 0.05 confidence level) in capture numbers between habitats (Table 1). Of the other four, Masked Yellowthroat (*Geothlypis aiquinoctialis*), Ultramarine Grosbeak (*Cyanocompsa brissonii*), and Dull-colored Grassquit (*Tiaris obscura*) were captured significantly more often in gallery forest, while Black-backed Grosbeak (*Pheucticus aureoventris*) was captured significantly more often in dry forest.

We captured 23 species (45% of species captured at the site) exclusively in gallery forest and 11 species (22%) exclusively in dry forest, a borderline significant difference between habitats (Binomial test, P = 0.059) (Table 2).

	Mist-net h	Number of species	Number of exclusive species ¹	Shannon Wiener Diversity ²	Seasonal species turnover ³	Number of individuals captured ⁴
Habitat						
Gallery forest (GF)	4498	40	23 (45%)	2.73	-	441 (0.10)
Dry forest (DF)	1712	28	11 (22%)	2.46	-	174 (0.10)
Season - habitat						
Dry season - GF	1791	32	2 (4%)	2.42	3 (9%)	164 (0.09)
Dry season - DF	915	18	5 (10%)	1.81	7 (39%)	114 (0.12)
Wet season - GF	2707	37	7 (14%)	2.31	8 (22%)	277 (0.10)
Wet season - DF	798	21	5 (10%)	2.75	10 (48%)	60 (0.08)

TABLE 2. Bird community patterns among habitats and seasons, based on capture data.

¹Number of species captured exclusively in a given habitat or season-habitat combination (and as a percent of species captured at the site).

²Diversity index after rarefaction (see Methods).

³Number of species captured in the season-habitat combination indicated but not in the same habitat in the opposite season (and as a percentage of the total number of species captured in that habitat).

⁴Total number of individuals captured in each habitat or season-habitat combination (and captures/nethr).

Captures by season and habitat. None of the species rarefaction curves for any season-habitat combination reached an asymptote (Fig. 4).

Expected species richness between seasons in dry forest was significantly higher in the wet season than the dry season. Furthermore, the



FIG. 2. Rarefaction curves of expected cumulative number of species for gallery and dry forest habitats, based upon captures in each habitat.

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FIG. 3. Mean number of expected species present in each habitat (seasons combined), after rarefaction. Error bars represent 95% confidence intervals. A significant difference between categories is indicated when letters above bars differ between categories.

dry season of the dry forest exhibited the lowest richness values of any season - habitat combination (Fig. 5). No significant difference in richness between seasons existed in gallery forest (Fig. 5). A larger difference in species diversity (Shannon-Weiner index) existed between seasons in dry forest, relative to gallery forest, with the dry season of the dry forest exhibiting the lowest value (Table 2). Seasonal species turnover (i.e., the number of species found exclusively in one season in a given habitat) was higher in the wet season in both habitats (Table 2). Nevertheless, in both seasons species turnover was higher in dry forest than in gallery forest (Table 2). Of the species captured exclusively in gallery forest, fewer species were captured only in the dry season relative to the wet season (two and seven species, respectively), while an equal number of species exclusive to the dry forest were captured in each season (Table 2).

Although capture rates across season – habitat combinations were relatively similar, capture rates in the dry forest during the dry

season were the highest of any season – habitat combination (Table 2).

DISCUSSION

Ecoregional affinity and habitat associations. While a majority of the avifauna recorded by both observations and captures in gallery and dry forest can be viewed as habitat generalists (i.e., 60% of species were found in both habitats), a notable proportion was associated exclusively with one habitat (20% with dry forest and 20% with gallery forest). Nevertheless, bird species in Neotropical dry forests and scrub are less likely to be restricted to a single habitat type than species of humid forest (Stotz *et al.* 1996). This tendency towards habitat generalism by birds occupying Neotropical dry forests may be a product of processes occurring at larger spatial scales.

Comparison of habitat occupancy at the site relative to the species' habitat affinities at a continental scale demonstrated that the Parapetí River gallery forest plays an important



FIG. 4. Rarefaction curves of expected cumulative number of species for dry and wet seasons in gallery and dry forest habitats, based upon captures in each season.

role in shaping avian community composition in the bolivian chaco by introducing into the region species that would likely not be present without the presence of the gallery forest, as has been shown in the chaco of Argentina (Nores 1992, but see Silva 1994).

Only 16 of the 1398 bird species recorded in Bolivia are considered by Hennessey et al. (2003) to be endemic to the chaco and only four of the species we recorded are considered by Hennessey et al. (2003) to be endemic to the bolivian chaco [Black-legged Seriema (Chunga burmeisteri), Chaco Owl (Strix chacoensis), Lark-like Bushrunner (Coryphistera alaudina), and Crested Gallito (Rhinocryipta lanceolata)]. According to Short (1975), the generally low level of avian endemism in the Gran Chaco can be accounted for by the lack of barriers to dispersal to and from the region. Because the chaco has been greatly modified historically by arid conditions alternating with very moist periods during the Pleistocene, Short (1975) hypothesized that the chaco avifauna is derived principally from other regions because the species currently inhabiting the chaco may have so recently colonized the region during such climatic cycles that sufficient time has not elapsed for differentiation to have occurred.

More recently, Herzog & Kessler (2002) documented biogeographical patterns among species of the bolivian chaco and adjacent Andean dry valleys, finding that although species richness levels are relatively low, the biogeographical affinities of birds in the bolivian chaco are varied. Additionally, a recent biogeographical analysis based on the raw distributions of 134 oscine taxa shows close affinities of the chaco with the pampas, cerrado and caatinga regions (Porzecanski & Cracraft 2005). Additional taxonomic and biogeographical data need to be collected and compared within a phylogenetic context.

Gallery-dry forest species captures. Measures of species richness using mist-nets are necessarily preliminary at this point. First, species sampling did not reach a clear asymptote after rarefaction (Fig. 2), suggesting the presence of some rare species and incomplete sampling of the community with mist-nets. Second, presence/absence of species based on both obser-



FIG. 5. Mean number of expected species in each habitat by season, after rarefaction. Error bars represent 95% confidence intervals.

vations and captures demonstrated that species richness was similar between the two habitats, while data from only captures indicated higher richness in gallery forest (Fig. 3). The fact that significantly fewer species were captured than were observed in dry forest while no such difference existed in gallery forest suggests a higher bias in sampling using mist-nets in dry forest than in gallery forest. Indeed, mist-netting does not sample all species with equal effectiveness (e.g., Remsen & Good 1996) and results of counts based on visual and acoustic cues often differ from those from mist-netting (Whitman et al. 1997, Derlindati & Caziani 2005, Estades et al. 2006). We believe three reasons could account for the observed differences in richness as measured by captures vs observations: 1) Because observations were made during walks occurring at a broader scale (i.e., kilometers) than that of mist nets (i.e., meters), capture data herein represent measures of richness occurring at a much more local scale than observations. Notably, many observations in dry forest occurred much closer to the river (less than one km) and more heavily

impacted by cattle than where mist-nets in the dry forest were located (5 km away from the river); 2) Micro-habitat use and behavior such as foraging height and flight distance may differ between the two habitats, since canopy height and vegetation structure between the two habitats varied (see Remsen & Good 1996); and 3) The asymptote for dry forest is still climbing, such that not all "catchable" species have been captured. This study is a good example of the different results capture vs. observational data can provide. Thus, results of mist-netting are preliminary, representing a subset of species and requiring further sampling in combination with other standardized methods such as point counts before definitive conclusions for each habitat can be determined. Nevertheless, some general patterns from capture data are notable.

The lower richness away from the river as indicated by capture data is a pattern mirrored in other studies that compared bird communities between riparian and non-riparian habitats in Australia (e.g., Bentley & Catterall 1997, Woinarsky *et al.* 2000, Palmer & Bennett 2006), and agrees with dry vs humid forest bird community patterns at larger scales in the Neotropics in which avian species richness is generally lower in dry forest than humid forest (Stotz *et al.* 1996). Diversity of species as measured by mist-netting was higher in gallery forest, a result that is similar to other studies of riparian vs. non-riparian bird communities (e.g., Strong & Bock 1990, Simmons & Allan 2002).

The number of species captured exclusively in gallery forest was more than double that of dry forest, although this difference may decrease with more sampling, since the species accumulation curve for dry forest had not reached an asymptote and observational data indicated that more species were present in both habitats. Nevertheless, 20% of species were recorded by observations and captures only in gallery forest. Furthermore, three species were captured significantly more often in gallery forest. These results support the conclusions of Stotz et al. (1996: 32) that the avifauna of the gallery forests of central South America shows habitat specialization to riverassociated forests such that this pattern is not restricted to Amazonia.

Other studies have also documented distinct habitat associations of mammals, amphibians and reptiles along the Parapetí River. Cuéllar & Noss (2003) found several mammal species that extend their ranges into the chaco via the Parapetí gallery forest: Capuchin monkey (*Cebus apella*), black howler monkey (*Alonatta caraya*) and crab-eating raccoon (*Procyon cancrivorus*) were found exclusively in this gallery forest. Gonzáles (1998) found several frog and snake species and one lizard species only in the Parapetí gallery forest.

In dry ecosystems, the generally more complex vegetation structure of riparian habitats relative to drier non-riparian habitats has been suggested to play a role in the higher species packing of birds in riparian habitats (e.g., Finch 1989, McGarigal & McComb 1992). Further research on the ecology of chaco birds, including their foraging, reproductive and dispersal strategies in gallery and dry forest, as well as environmental parameters such as vegetation structure and food availability in each habitat, would shed light on the factors that influence bird community structure in these habitats. An interesting comparative study on the role of riparian habitat in structuring local bird communities in the Neotropics would be between riparian forests in different ecoregions (e.g., caatinga vs chaco).

Season-habitat species captures. Patterns of species richness as measured by captures across habitats and seasons suggest that seasonal bird community composition at the site exhibits substantial change, especially in the dry forest. First, species richness of the dry forest was significantly lower in the dry season than in the wet season and lower than gallery forest species richness in either season. Second, seasonal species turnover was much higher in dry forest than in gallery forest, suggesting a more stable bird community composition between seasons in the gallery forest. We cannot rule out that some of these species may be less "catchable" in one season than another due to behavioral differences. However, the dry forest also had a higher capture rate in the dry season than in the wet season, which could be an artifact of a change in the probability of species being captured between seasons if their seasonal activity patterns vary. For example, birds may have to increase foraging effort - resulting in a higher capture rate in the dry forest in the dry season - if food resources in the dry season are more patchy and limited there (which would not be surprising given the strong seasonality of the dry forest, in which very little fruit or insects were apparent in the dry season (A. Jahn pers. observ.). For other species only captured in the dry forest

in the wet season, seasonal dispersal between habitats may be a way around this problem. These possibilities are speculative at this point but could prove to be an interesting future line of research focused on the constraints these species face between seasons and habitats.

Dry forests are considered to be the most threatened of all forest types in the Neotropics (Gentry 1977, 1993, Janzen 1988). The bolivian chaco represents only a small portion (11.6%) of the Gran Chaco, but with Kaa-Iya and Otuquis National Parks, it holds approximately half of the protected land area of the entire Gran Chaco ecoregion (The Nature Conservancy et al. 2005). Indeed, compared to the chaco forests of Paraguay and northern Argentina, where there is an ever-increasing level of habitat destruction (Morello & Hortt 1985, Taber 1991), the bolivian chaco is likely the least altered (Parker et al. 1993). This could change in the near future, as a recent conservation evaluation of the Gran Chaco by The Nature Conservancy et al. (2005) identified major threats to the bolivian chaco: gas and petroleum exploitation, expansion of highways and roads, agriculture and fire.

Increasing evidence suggests that the gallery forest, in spite of its smaller size relative to the surrounding dry forest, holds a notable proportion of bird species exclusive to it locally (20%), and may therefore play an important role in the evolutionary history of the local avian community, as has been shown for gallery forests in the brazilian cerrado habitat for birds (Silva 1995, Silva & Bates 2002, Piratelli & Blake 2006) and mammals (Redford & da Fonseca 1986). This, plus the limited extent of the gallery forest and relatively high human densities (mainly native Guaraní) in the Parapetí gallery forest relative to the surrounding dry forest (A. Noss pers. com.), suggest that conservation planning in this region should prioritize the gallery forest system for protection and management.

Given the growing human pressure on the natural resources of the bolivian chaco, conservation planning must go hand-in-hand with sustainable development, prioritizing habitats and ecosystem processes for protection while simultaneously respecting human needs and fostering improved quality of life in local human communities.

ACKNOWLEDGMENTS

We thank the owner of San Julian, Alfonso Roda, for his hospitality during our visits to his property. A.L. Porzecanski received generous support from the Frank M. Chapman Memorial Fund at the AMNH, Columbia University, and the AMNH's Center for Biodiversity and Conservation (NASA Grant no. NAG5-8543). A.E. Jahn received support from the Association of Field Ornithologists and Manomet Center for Conservation Sciences. R. Dobbs was supported through a National Science Foundation grant to D. J. Levey and J. J. Tewksbury (DEB 0129168). We thank Dennis Lichtenberg, Jeremy Macik, Doug Meredith, Amanda Marsh, John Prather and Rosa Strem for help with data collection and management. John Bates, Jesus Guerrero, Doug Levey, Andrew Noss and two anonymous reviewers provided many helpful comments, which greatly improved the manuscript.

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