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RESPONSES OF AVIAN ASSEMBLAGES TO A NATURAL EDGE IN A CHACO SEMIARID FOREST IN ARGENTINA

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ABSTRACT.—We assessed differences in breeding bird assemblages and vegetation structure between a natural forest edge and the adjacent forest interior in an old-growth Chaco forest of Argentina. The edge had a dense cover of thin stems at low heights and high species richness of woody plants, whereas the interior had high canopy cover, high tree density, high density of thick stems, and a more heterogeneous vertical profile. We used mist-net and point-count surveys to sample bird assemblages, capturing 374 birds during 3,553 net hours and detecting 826 individuals during point counts. Overall, we recorded a total of 74 bird species. Bird species richness and bird abundance appeared to be higher in the edge, although differences between habitats were not entirely consistent for mist-net and point-count data. Several early successional bird species were closely associated with edge, and other species occurred exclusively in the interior of the forest. At the guild level, frugivores, terrestrial granivores, arboreal granivores, terrestrial insectivores, and long-flight insect-hunters were more abundant at the edge than in the interior, whereas the reverse was true for bark insectivores and short-flight insectivores. Our results indicate that edge and interior bird assemblages are different. The distribution of birds between these habitats appeared to reflect constraints on habitat use imposed by vegetation structure, and also could be related to differential distribution of food resources, especially fruit. *Received 27 February 1997, accepted 11 November 1997.*

MICROCLIMATIC AND STRUCTURAL CONDITIONS at forest edges usually are associated with a change in density and diversity of birds and other animals, a phenomenon frequently called "edge effect" (Reese and Ratti 1988, Alverson et al. 1988, Yahner 1988). For decades, edge habitats were considered beneficial (e.g. to some cervids and game birds), and several management practices were based on this principle (Reese and Ratti 1988). However, edge conditions are detrimental to some forest-interior specialists (Gates and Gysel 1978, Whitcomb et al. 1981, Brittingham and Temple 1983, Lovejoy et al. 1986, Paton 1994, King et al. 1996). Thus, forest exploitation that results in extensive clearings increases the amount of edge habitat and may adversely affect forest-dwelling species (Wilcove et al. 1986, Rolstad 1991, Saunders et al. 1991, Harris and Silva-Lopez 1992, Faaborg et al. 1993, Murcia 1995). Knowledge of changes in avian assemblages from edge habitats to the forest interior may help to predict how fragmentation will affect the composition and organization of forest avifaunas.

Most studies of edge effects on birds have dealt with anthropogenic boundaries. These edges often are recent, abrupt, and exposed to the surrounding environment; over time, they close as vegetation quickly fills in the open habitat (Ranney et al. 1981, Wiliams-Linera 1990). Therefore, the abiotic and structural conditions at older (e.g. natural) edges are different from those at newly created edges (Ranney et al. 1981; Williams-Linera 1990; Matlack 1993, 1994). Furthermore, different edge types can be related to a variety of responses of bird populations (Noss 1991, Murcia 1995, Hawrot and Niemi 1996). Notwithstanding, comparatively few studies have focused on the effect of natural forest edges on birds (Helle and Helle 1982, Noss 1991).

The Chaco is a vast plain of dry scrub and deciduous forest in south–central South Amer-

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ica. Although the status and distribution of Chaco birds have been well studied (e.g. Short 1975), little is known about the ecology of avian assemblages in this region. In particular, the effect of forest edges on these birds has never been assessed. Here, we analyze the responses of bird populations and guilds to a natural edge in a Chaco semiarid forest, relating differences between edge and interior assemblages with vegetation structure of both environments. We focus on the following questions: (1) Does the bird assemblage differ between the interior and the edge? (2) What are the specific changes in abundance of species and guilds from the edge to the interior? (3) Are differences in bird assemblages between habitats meaningfully explained by vegetation structure?

STUDY AREA AND METHODS

Study area.—The study area was in the Copo Natural Reserve (25°55′S, 62°05′W; elevation 170 m), Province of Santiago del Estero, Argentina. The reserve encompasses about 114,000 ha and lies within the Occidental District of the Chacoan Biogeographic Province (Cabrera and Willink 1980). Nearly two-thirds of the area of the reserve consists of a single tract of old-growth xerophytic forest ("Quebrachal of two quebrachos;" see Prado 1993), which continues toward the north in a remarkably homogeneous fashion for hundreds of kilometers and comprises the largest pristine area of Chaco semiarid forest in Argentina. Large tracts of second-growth forest (selectively logged in the 1950s) occur on the southwestern portion of the reserve, and most southern and southwestern lands outside the reserve are subjected to diverse threats, including logging and clearing of second-growth forests for agriculture and cattle grazing.

The old-growth forest is dominated by red quebracho (*Schinopsis quebracho-colorado;* Anacardiaceae), white quebracho (*Aspidosperma quebracho-blanco;* Apocynaceae), and mistol (*Ziziphus mistol;* Rhamnaceae). *Capparis retusa* (Capparidaceae) and the thorny shrubs *Acacia praecox* (Leguminosae), *Celtis pallida* (Ulmaceae), and *Castela coccinea* (Simaroubaceae) characterize the shrub layer (Lopez de Casenave et al. 1995). The forest in this region is frequently interrupted by belts (ca. 1 km wide) of natural grasslands (*Elionurus* spp.). These grasslands, or "caños," grow in ancient river beds filled with aluvial sands (Morello and Adamoli 1974, Prado 1993). Therefore, the grassland-forest boundary is controlled by edaphic factors.

The climate is continental semiarid and highly seasonal, with a distinct dry season in autumn/winter (April to September) and a warm wet season in spring/summer (October to March). Mean annual temperature is near 22°C, with a mean maximum temperature of more than 35°C. During summer, we recorded an absolute maximum temperature of 46°C in the forest, whereas absolute minimum temperatures fell below −7°C in winter. Mean annual precipitation is 635 mm (Morello and Adamoli 1974), about 80% of which falls between October and March (Short 1975), although year-to-year variation in rainfall is high.

Our study site encompassed about 23 ha and was located in old-growth forest adjacent to a belt of natural grassland. Sampling was conducted along the border (forest edge, ca. 350 m long) and inside the forest. We considered as "edge" the 20-m-wide belt that constitutes the border of the forest. The forest interior was sampled at least 200 m from the border.

Vegetation.—Seven plots (15 × 15 m) were randomly located in the edge and seven in the interior of the forest during September to October in 1991. In each plot, we recorded diameter at breast height (dbh) of trees and basal diameter (dbs) at 20 cm height of each stem of shrubs and saplings. We were able to analyze separately both the shrub (0 to 4 m) and the arboreal strata (>4 m), provided that those trees with dbh >4.5 cm reached heights of more than 4 m, and thus contributed to the arboreal layer (see Lopez de Casenave et al. 1995). For each plot, we calculated values of the following features of horizontal structure and cover: basal area by stratum (shrub and arboreal), total number of trees, number of trees with dbh >20 cm, number of stems in each of two size classes (<5 cm dbs and 5 to 20 cm dbs), number of woody species, and stem diameter diversity (SDD). SDD was calculated as $1/\Sigma\, p_i^2$, where p_i represents the proportion of all stems with diameters in the *i*th diameter class, based on 5-mm size classes.

Vertical structure was measured along 16 transects, each 15 m long, during March 1992. Eight transects were randomly located on the edge (perpendicular to the border), and eight were randomly located in the forest interior. We sampled the shrub stratum at 60 random points on each transect by erecting a rod marked at 1-m intervals and recording the height of contacts of the woody vegetation on the rod. We sampled the arboreal stratum at 15 random points on each transect, but here the rod was marked at 2-m intervals. Foliage height diversity (FHD) was calculated as $1/\Sigma\, p_i^2$, where p_i is the proportion that represent coverage of height interval i with respect to total coverage of the profile.

Vegetation sample plots and transects were established throughout the mist-netting area. However, we did not measure vegetation at bird sampling sites because the operation of mist nets sometimes disturbed the physical structure of the vegetation.

Birds.—Mist-net and point-count surveys were used to sample the bird assemblage during the middle (December) and late (February to March) breeding season of 1990–91. Mist nets are efficient for comparisons among sites because they allow an identical and simultaneous sampling (Karr 1979, 1981), whereas point counts provide additional information about species undersampled by mist nets. This combination of sample procedures has been used successfully in other studies (e.g. Wong 1985, Lynch 1989, Blake and Loiselle 1992).

We used 16 mist nets (2 m height, 6 m length, four shelves) at eight randomly selected sample sites in the interior of the forest, and 16 nets at eight randomly selected sites at the edge. Sample sites were spaced 70 to 100 m apart in the interior and 50 to 70 m apart at the edge. We placed two nets at each site (both roughly perpendicular to the border at the edge), one with 36-mm mesh and another with 60-mm mesh. This procedure increases sampling efficiency because nets of different mesh sizes preferentially capture different-sized birds (Karr 1979, 1981, Pardieck and Waide 1992). Nets were opened at dawn, checked every hour, and closed at about 1200 each day (and during periods of heavy rain). Birds were banded and released in the vicinity of capture. We used the number of birds captured per 100 mist-net hours as an index of bird abundance at each sample site. Recaptured birds (<5% of the total) were not included in the analyses. Birds were mist-netted for 10 nonconsecutive days during December 1990 and for 14 nonconsecutive days during February to March 1991.

We counted birds at four sample points located randomly in the edge and at four points located randomly in the forest interior. Points were spaced 100 to 150 m apart. Each 30-min count began 1 min after observers reached the sample point to allow the birds to settle. Two observers recorded birds within a radius of 10 m from the center of the sample point; we were especially cautious to establish edge points encompassing only the edge habitat. We did not record birds flying above the canopy. We made counts for six consecutive days in December 1990 and for nine nonconsecutive days during February to March 1991. All counts were conducted between dawn and 1000, and the order in which sample points were visited was rotated daily. We considered the average number of individuals detected as a measure of bird abundance at each sample point.

Bird species were classified into eight guilds: (1) frugivores, (2) terrestrial granivores, (3) arboreal granivores, (4) foliage insectivores, (5) terrestrial insectivores, (6) bark insectivores, (7) short-flight insect-hunters, and (8) long-flight insect-hunters. The assignment of species was based on an analysis of fecal samples (Caziani 1996), our own observations of foraging sites and behavior (Lopez de Casenave 1994), and published reports (e.g. Short 1975, Kratter et al. 1993).

Frugivores usually consume fruit, although most of them also consume insects to some degree. During the breeding season, however, all of them depend heavily on the fleshy fruits of several species of plants (Caziani 1996). Granivores feed primarily on seeds on the ground (terrestrial granivores) or in trees (arboreal granivores), but some terrestrial granivores also consume insects (Short 1975). Foliage insectivores eat insects by gleaning from and hovering at leaves and twigs, short-flight insect-hunters use hovers and short (mean attack distance 0.85 m) sallies, whereas long-flight insect-hunters chase their prey with long (mean distance 5.48 m) sallies (Lopez de Casenave 1994). Finally, terrestrial and bark insectivores glean insects from the ground and probe into trunks and thick stems, respectively. Lopez de Casenave (1994) provides a more detailed description of guild characteristics and bird species assignments.

Differences in bird abundance and species richness between edge and interior sites were evaluated with Mann-Whitney *U*-tests. The cumulative number of species was compared between the edge and interior using the Yates' corrected X^2 goodness-of-fit test. All statistical analyses were carried out separately for mist-net and point-count data. Small sample sizes resulted in an increase of Type II errors and low power of the tests. Because Type II errors can be more costly than Type I errors in environmental research (Shrader-Frechette and McCoy 1993, Smith 1995, Steidl et al. 1997), we used an alpha level of 0.10 when interpreting our results.

RESULTS

Vegetation.—Basal area of the canopy and subcanopy (i.e. arboreal layer) and basal area of the shrub layer were not significantly different between interior and edge habitats (Table 1). Tree abundance per plot increased nearly twofold from the edge to the interior. This difference was associated with a reduced abundance of medium-sized trees at the edge, because large trees (>20 cm dbh) were present in similar numbers in both habitats. Thin branches (<5 cm dbs) were significantly more abundant in edge plots, whereas abundance of thick stems (5 to 20 cm dbs) was higher in the interior. Stem diameter diversity was similar in both sites, but species richness of woody plants was significantly higher on the edge (Table 1).

The vertical structure of the vegetation differed between sites (Fig. 1). Cover up to 1 m was significantly higher in the edge, whereas cover above 8 m was significantly higher in the interior. These differences resulted from higher densities of low shrubs at the edge and higher

TABLE 1. Forest edge and forest interior vegetation characteristics at Copo Natural Reserve, Argentina. Values are $\bar{x}$ ± SE ($n = 7$ plots).

Variable	Edge	Interior	P[a]
Basal area by stratum (m^2/ha)			
Arboreal layer	11.66 ± 1.65	14.59 ± 2.13	ns
Shrub layer	9.99 ± 1.22	9.02 ± 0.51	ns
Tree abundance (number/plot)			
Total	6.43 ± 1.70	12.00 ± 1.27	*
Trees >20 cm dbh	2.86 ± 0.46	3.43 ± 0.48	ns
Stem abundance (number/plot)			
<5 cm dbs	1,079.14 ± 84.33	583.14 ± 80.22	**
5 to 20 cm dbs	19.86 ± 3.78	34.57 ± 1.45	**
Stem diameter diversity	4.20 ± 0.31	5.11 ± 0.71	ns
Species richness (species/plot)	16.71 ± 0.42	13.57 ± 0.30	***

[a] *, $P < 0.05$; **, $P < 0.005$; ***, $P < 0.001$; ns, not significant (Mann-Whitney U-test).

abundance of trees in the interior (Lopez de Casenave et al. 1995). Foliage height diversity was significantly higher in the interior (5.36 vs. 4.59; Mann-Whitney U-test, $P < 0.05$, $n = 8$) due to a more equitable distribution of cover among height classes in the interior of the forest.

Birds.—We recorded a total of 74 bird species (Table 2). We captured 374 individuals (excluding recaptures) during 3,553 mist-net hours and detected 826 individuals during point counts. The shape of the cumulative curves of number of species recorded or captured versus sampling effort (Fig. 2) suggests that our samples adequately quantified the presence of species.

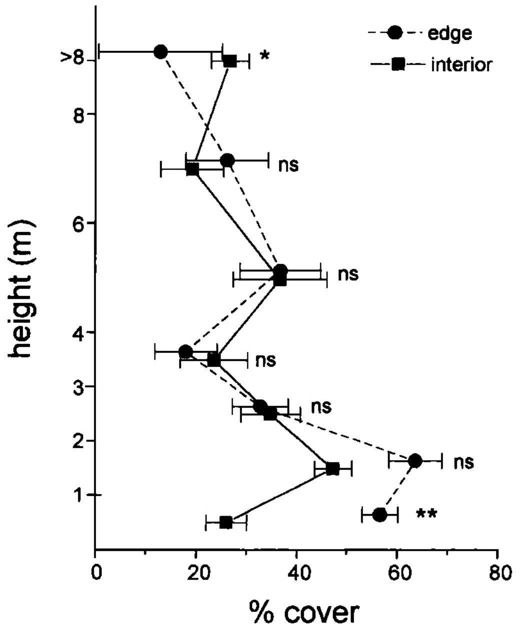

FIG. 1. Foliage cover profiles ($\bar{x}$ ± SE; $n = 8$) for the interior and edge of the forest at Copo Natural Reserve, Argentina. Percent cover represents the percentage of vegetation contacts at a given height interval. Results of Mann-Whitney U-tests for differences between means at each height interval are indicated (*, $P < 0.01$; **, $P < 0.001$; ns, not significant).

Bird species richness and bird abundance appeared to be higher in the edge, although differences between habitats were not entirely consistent for mist-net and point-count data. The mean number of captures per 100 mist-net hours was higher for edge nets (12.41 ± SE of 1.49) than for interior nets (8.63 ± 0.84; Mann-Whitney U-test, $P = 0.059$, $n = 8$), but there were no significant differences between habitats in the average number of birds detected per sample point (9.55 ± 2.10 in the edge vs. 5.40 ± 0.63 in the interior; Mann-Whitney U-test, $P = 0.149$, $n = 4$). Furthermore, mean species richness per sample site did not differ between edge (12.25 ± 1.61) and interior (10.50 ± 0.96) for mist-net data (Mann-Whitney U-test, $P = 0.367$, $n = 8$), but the mean number of species detected per sample point in counts was higher in the edge (29.00 ± 2.27) than in the interior (21.50 ± 2.02; Mann-Whitney U-test, $P = 0.080$, $n = 4$). There were no significant differences between habitats in either the cumulative number of species captured in nets (40 in the edge vs. 35 in the interior; $X^2 = 0.21$, df = 1, $P = 0.647$), or in the cumulative number of species recorded in counts (57 vs. 40; $X^2 = 2.64$, df = 1, $P = 0.104$).

Twenty-eight species were captured more often in edge nets (although differences were not necessarily significant) than in interior nets, whereas 16 species were caught more often in the interior. In point counts, 40 species were recorded more often in the edge, whereas 22 were recorded more often in the interior. Fourteen species were captured only in the edge, and nine species were captured only in interior nets. In point counts, 26 species were detected only in the edge, and 9 species were detected only in the forest interior.

Five of the 47 species (10.6%) captured in nets showed significant differences between habitats in the mean number of captures per 100 mist-net hours (Table 2). Less than three species (0.05 × 47) would be expected to show a significant difference by chance alone. Furthermore, 12 of the 64 species (18.8%) recorded in point counts showed significant differences between the edge and the interior (Table 2). By chance, less than four species (0.05 × 64) would be expected to show such differences. It should be noted, however, that 13 of the 14 species with statistically significant differences between sites (Table 2) were more abundant in the edge, whereas only 1 species was more abundant in the interior of the forest.

Frugivores, granivores (both terrestrial and arboreal), terrestrial insectivores, and long-flight insect-hunters were significantly more abundant at the edge than in the interior, whereas bark insectivores and short-flight insect-hunters were more abundant in the interior (Table 3).

DISCUSSION

Edge effects.—Forest edges often support a characteristic set of bird species (Johnston 1947, Cieslak 1992). We found a difference in species composition between interior and edge habitats, and more species with unequal abundance between habitats, than would be expected by chance. Our results indicate that edge and interior assemblages are different. Several species occurred in the edge but were not present in the interior (e.g. *Tyrannus melancholicus, Saltatricula multicolor*), but we also found species exclusive to the interior of the forest, mainly bark insectivores (e.g. woodcreepers). The pattern of abundance within guilds also differed between habitats: bark insectivores and short-flight insect-hunters were more abundant in the interior, whereas long-flight insect-hunters, frugivores, terrestrial insectivores, and granivores were more abundant in the edge.

Increased densities of individuals and species are the most frequent "edge effects" observed in temperate forests in North America and Europe (e.g. Johnston 1947, Hansson 1983, Yahner 1987, Cieslak 1992). Most of these studies were carried out in anthropogenic edges, in contrast to the natural edge we studied. Recently created, artificial edges may differ in structure from older edges (Ranney et al. 1981, Williams-Linera 1990). The edge we studied presumably resembled these older edges because it was a natural border that had existed for a long time. Therefore, it was a "mature edge" (sensu Ranney et al. 1981) that constituted a true ecotone between two distinct habitats (forest and grassland). Differences in avian assemblages, however, did not appear to be the result of an ecotonal effect (i.e. a juxtaposition of grassland and forest assemblages), because no one species with a significant difference in abundance between habitats was primarily a grassland bird. A few grassland-dwelling species occasionally were recorded in our samples (e.g. *Volatinia jacarina, Aimophila strigiceps, Ammodramus humeralis*), but most of the species considered in this study were forest or shrubland birds.

Edge and interior habitats.—Vegetation structure was markedly different between habitats. The forest edge had a very dense cover of thin branches at low heights, whereas the interior provided more trees and higher canopy cover. Higher vegetation density at edges enhances the availability of cover, food resources, and nesting sites, thus promoting increased bird densities (Helle and Helle 1982, Fuller and Whittington 1987). More directly, however, edge vegetation offers a greater diversity of foraging opportunities. High shrub cover should favor foraging maneuvers involving passive searching among the foliage, and open canopy should facilitate the use of long flights. Greater abundance of frugivores and long-flight insect-hunters in the edge may be the result. On the other hand, reduced foliage cover in the forest interior results in open spaces among plants at intermediate strata, which should favor the use of short- and moderate-length flights and hovering, thus promoting increased numbers of short-flight insect-hunters that are less able to cope with the dense thickets at edges. Further-

TABLE 2. Guild assignments and abundances of bird species in edge and interior forest at Copo Natural Reserve, Argentina. Values are $\bar{x}$ ± SE for captures/100 mist-net hours ($n = 8$ sample sites) and number of birds detected per sample point ($n = 4$ sample points).

	Nets			Counts		
Species[a]	Edge	Interior	*P*[b]	Edge	Interior	*P*[b]
Spiziapteryx circumcinctus (O)	—	—	—	0.06 ± 0.04	—	ns
Ortalis canicollis (F)	—	—	—	0.05 ± 0.05	—	ns
Columba spp.[c] (TG)	—	—	—	0.17 ± 0.08	0.07 ± 0.03	ns
Zenaida auriculata (TG)	—	—	—	0.26 ± 0.16	0.09 ± 0.05	ns
Columbina picui (TG)	0.45 ± 0.15	0.28 ± 0.12	ns	0.46 ± 0.19	0.19 ± 0.11	ns
Aratinga acuticaudata (AG)	—	—	—	—	0.03 ± 0.02	ns
Myiopsitta monacha (AG)	—	—	—	0.08 ± 0.08	—	ns
Amazona aestiva (AG)	—	—	—	0.09 ± 0.05	0.12 ± 0.07	ns
Coccyzus americanus (FI)	—	0.06 ± 0.06	ns	0.02 ± 0.02	—	ns
Coccyzus melacoryphus (FI)	—	—	—	0.04 ± 0.04	—	ns
Glaucidium brasilianum (O)	—	0.05 ± 0.05	ns	0.02 ± 0.02	—	ns
Caprimulgus parvulus (O)	0.51 ± 0.10	0.28 ± 0.14	ns	—	—	—
Heliomaster furcifer (O)	0.06 ± 0.06	0.05 ± 0.05	ns	0.04 ± 0.02	—	ns
Chlorostilbon aureoventris (O)	—	—	—	0.02 ± 0.02	0.05 ± 0.02	ns
Nystalus maculatus (SF)	—	0.05 ± 0.05	ns	—	—	—
Colaptes melanolaimus (BI)	0.06 ± 0.06	0.11 ± 0.07	ns	0.05 ± 0.05	0.12 ± 0.08	ns
Picoides mixtus (BI)	—	0.06 ± 0.06	ns	0.04 ± 0.02	—	ns
Campephilus leucopogon (BI)	—	—	—	0.04 ± 0.02	0.02 ± 0.02	ns
Xiphocolaptes major (BI)	0.05 ± 0.05	0.05 ± 0.05	ns	0.04 ± 0.04	—	ns
Drymornis bridgesii (BI)	—	0.11 ± 0.07	ns	—	—	—
Lepidocolaptes angustirostris (BI)	—	—	—	—	0.04 ± 0.04	ns
Campylorhamphus trochilirostris (BI)	—	—	—	—	0.02 ± 0.02	ns
Sittasomus griseicapillus (BI)	—	0.06 ± 0.06	ns	—	0.05 ± 0.05	ns
Furnarius rufus (TI)	0.23 ± 0.12	0.22 ± 0.22	ns	—	0.22 ± 0.06	**
Furnarius cristatus (TI)	—	—	—	0.02 ± 0.02	—	ns
Cranioleuca pyrrhophia (FI)	0.17 ± 0.08	—	*	0.08 ± 0.08	0.08 ± 0.06	ns
Coryphistera alaudina (TI)	0.12 ± 0.08	—	ns	0.07 ± 0.04	—	ns
Asthenes baeri (FI)	0.06 ± 0.06	—	ns	—	—	—
Synallaxis frontalis (FI)	0.11 ± 0.11	—	ns	—	0.04 ± 0.04	ns
Thamnophilus caerulescens (FI)	0.05 ± 0.05	0.27 ± 0.11	ns	0.08 ± 0.03	0.02 ± 0.02	*
Taraba major (TI)	0.11 ± 0.07	—	ns	0.02 ± 0.02	—	ns
Myrmorchilus strigilatus (TI)	0.11 ± 0.08	0.05 ± 0.05	ns	0.04 ± 0.04	0.04 ± 0.04	ns
Pachyramphus polychopterus (SF)	—	0.16 ± 0.11	ns	—	—	—
Pachyramphus viridis (SF)	—	—	—	0.04 ± 0.04	0.02 ± 0.02	ns
Knipolegus striaticeps (SF)	0.40 ± 0.18	0.55 ± 0.14	ns	0.11 ± 0.09	0.66 ± 0.36	ns
Myiodynastes maculatus (SF)	—	—	—	0.11 ± 0.05	0.30 ± 0.10	ns
Tyrannus melancholicus (LF)	—	—	—	0.35 ± 0.20	—	**
Tyrannus savana (LF)	—	—	—	0.06 ± 0.06	—	ns
Empidonomus aurantioatrocristatus (LF)	0.06 ± 0.06	—	ns	1.58 ± 0.43	0.48 ± 0.21	**
Casiornis rufa (SF)	—	0.11 ± 0.07	ns	0.02 ± 0.02	0.05 ± 0.03	ns
Myiarchus spp.[d] (LF)	0.34 ± 0.11	0.28 ± 0.14	ns	0.37 ± 0.15	0.38 ± 0.07	ns
Cnemotriccus fuscatus (SF)	0.05 ± 0.05	0.05 ± 0.05	ns	—	0.13 ± 0.13	ns
Sublegatus modestus (SF)	0.12 ± 0.12	0.11 ± 0.07	ns	0.02 ± 0.02	—	ns
Suiriri suiriri (SF)	0.06 ± 0.06	—	ns	0.04 ± 0.02	0.24 ± 0.16	ns
Myiophobus fasciatus (SF)	0.23 ± 0.09	0.05 ± 0.05	*	—	—	—
Todirostrum margaritaceiventer (SF)	0.11 ± 0.07	0.05 ± 0.05	ns	0.06 ± 0.04	0.07 ± 0.07	ns
Euscarthmus meloryphus (SF)	0.12 ± 0.08	0.06 ± 0.06	ns	0.11 ± 0.03	—	**
Stigmatura budytoides (FI)	0.06 ± 0.06	0.06 ± 0.06	ns	0.17 ± 0.10	—	ns
Elaenia spp.[e] (F)	0.97 ± 0.29	1.05 ± 0.24	ns	0.61 ± 0.13	0.17 ± 0.10	**
Troglodytes aedon (FI)	0.06 ± 0.06	—	ns	0.02 ± 0.02	—	ns
Turdus amaurochalinus (F)	3.02 ± 0.66	2.26 ± 0.26	ns	0.90 ± 0.37	0.12 ± 0.02	**
Polioptila dumicola (FI)	0.05 ± 0.05	0.06 ± 0.06	ns	0.29 ± 0.09	0.41 ± 0.17	ns
Vireo olivaceus (FI)	0.86 ± 0.32	0.39 ± 0.13	ns	0.19 ± 0.12	0.20 ± 0.17	ns
Cyclarhis gujanensis (FI)	—	0.11 ± 0.07	ns	—	0.07 ± 0.04	ns
Parula pitiayumi (FI)	—	—	—	0.20 ± 0.10	0.36 ± 0.12	ns
Thraupis sayaca (O)	0.06 ± 0.06	—	ns	0.02 ± 0.02	—	ns

TABLE 2. Continued.

Species[a]	Nets Edge	Nets Interior	Nets P^b	Counts Edge	Counts Interior	Counts P^b
Thraupis bonariensis (O)	—	—	—	0.06 ± 0.06	0.02 ± 0.02	ns
Piranga flava (O)	—	—	—	—	0.10 ± 0.06	ns
Saltator aurantiirostris (AG)	0.51 ± 0.18	0.05 ± 0.05	**	0.41 ± 0.12	0.02 ± 0.02	**
Paroaria coronata (AG)	0.06 ± 0.06	—	ns	0.07 ± 0.04	—	ns
Cyanocompsa brissonii (TG)	—	—	—	0.02 ± 0.02	—	ns
Volatinia jacarina (TG)	—	—	—	0.04 ± 0.04	—	ns
Tiaris obscura (TG)	0.06 ± 0.06	0.11 ± 0.07	ns	—	—	—
Coryphospingus cucullatus (TG)	2.51 ± 0.61	1.11 ± 0.27	*	0.67 ± 0.20	0.08 ± 0.04	**
Aimophila strigiceps (TG)	0.06 ± 0.06	—	ns	0.02 ± 0.02	—	ns
Zonotrichia capensis (TG)	0.12 ± 0.08	0.28 ± 0.12	ns	0.24 ± 0.09	0.02 ± 0.02	**
Ammodramus humeralis (TG)	0.06 ± 0.06	—	ns	0.04 ± 0.04	—	ns
Poospiza melanoleuca (FI)	0.22 ± 0.14	—	ns	0.62 ± 0.17	0.21 ± 0.08	*
Saltatricula multicolor (TG)	0.17 ± 0.08	—	*	0.18 ± 0.09	—	**
Icterus cayanensis (FI)	—	—	—	0.02 ± 0.02	0.12 ± 0.07	ns
Molothrus bonariensis (TI)	—	—	—	0.09 ± 0.05	—	ns

[a] Guild abbreviations: F, frugivores; TG, terrestrial granivores; AG, arboreal granivores; FI, foliage insectivores; TI, terrestrial insectivores; BI, bark insectivores; SF, short-flight insect-hunters; LF, long-flight insect-hunters; O, other guilds.

[b] *, $0.05 < P < 0.10$; **, $0.01 < P < 0.05$; ns, not significant (Mann-Whitney *U*-test).

[c] Including *Columba maculosa* and *C. picazuro*.

[d] Including *Myiarchus swainsoni* and *M. tyrannulus*.

[e] Including *Elaenia parvirostris* and *E. albiceps*.

more, the higher abundance of bark insectivores in the interior of the forest may be related to the increased density of trees in this habitat.

Circumstantial evidence suggests that food abundance is an important factor that influences the distribution of birds in both habitats. Forest edges usually support high seed and propagule densities (Ranney et al. 1981) and increased abundance of insects (Lovejoy et al. 1986, Fowler et al. 1993). In addition, edge-related plants frequently show higher fruit production and longer fruiting periods than interior ones (McDiarmid et al. 1977). In our study site, the edge had higher densities and basal areas of plant species bearing fleshy fruits that are consumed by frugivores (e.g. *Celtis pallida, Achatocarpus praecox*; Lopez de Casenave et al. 1995), and individual edge plants provide higher fruit numbers than interior ones (Caziani 1996). Thus, greater abundance of several guilds at the edge (especially frugivores) might also reflect high concentrations of food resources there.

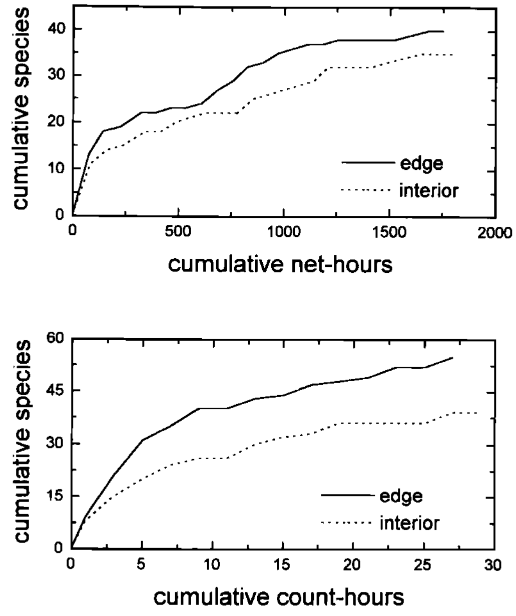

FIG. 2. Cumulative number of bird species captured in mist nets (upper panel) and recorded in point counts (lower panel) in the interior and edge of the forest at Copo Natural Reserve, Argentina.

Besides the responses of birds to vegetation structure and the potential importance of food availability, other factors that we did not examine could be associated with differences in bird abundance between habitats. In particular, further research is needed to determine the importance of microhabitat selection based on differential microclimatic conditions between forest sites, the availability of nest sites, and the role of predation pressure and social or interspecific interactions.

Table 3. Guild abundance in edge and interior forest at Copo Natural Reserve, Argentina. Values are $\bar{x} \pm$ SE for captures/100 mist-net hours ($n = 8$ sample sites) and number of birds detected per sample point ($n = 4$ sample points).

	Nets			Counts		
Guilds	Edge	Interior	P^a	Edge	Interior	P^a
Frugivores	3.99 ± 0.73	3.31 ± 0.41	ns	1.56 ± 0.51	0.29 ± 0.09	**
Terrestrial granivores	3.41 ± 0.71	1.77 ± 0.29	*	2.09 ± 0.62	0.45 ± 0.17	*
Arboreal granivores	0.57 ± 0.17	0.05 ± 0.05	***	0.65 ± 0.24	0.17 ± 0.10	*
Foliage insectivores	1.64 ± 0.51	0.95 ± 0.25	ns	1.71 ± 0.31	1.51 ± 0.45	ns
Terrestrial insectivores	0.58 ± 0.17	0.27 ± 0.22	*	0.24 ± 0.04	0.26 ± 0.03	ns
Bark insectivores	0.11 ± 0.07	0.39 ± 0.13	*	0.17 ± 0.05	0.24 ± 0.11	ns
Short-flight insect-hunters	1.09 ± 0.26	1.22 ± 0.28	ns	0.50 ± 0.08	1.46 ± 0.16	**
Long-flight insect-hunters	0.39 ± 0.13	0.28 ± 0.14	ns	2.36 ± 0.81	0.86 ± 0.27	*
Other guilds	0.62 ± 0.14	0.39 ± 0.17	ns	0.21 ± 0.07	0.17 ± 0.08	ns

[a] *, $0.05 < P < 0.10$; **, $0.01 < P < 0.05$; ***, $P < 0.01$; ns, not significant (Mann-Whitney U-test).

Conservation implications.—Despite the apparent increase in the density of birds at the edge, the significantly higher abundance of some guilds and species in the interior suggests that edge conditions were unsuitable for these birds. This situation has been reported in other studies (Whitcomb et al. 1981, Kroodsma 1982, 1984, Noss 1991, Faaborg et al. 1993), especially for birds that nest in North America and migrate to the Neotropics (Whitcomb et al. 1981, Hagan and Johnston 1992, Finch and Stangel 1993; but see Thompson et al. 1992).

Our results cannot be extrapolated beyond our study plot because we looked at only one natural forest edge. Nonetheless, a comparison of our data with those of previous studies in this area can help to illuminate the potential outcome of some human influences on this forest. The avian assemblage in the edge habitat in our study site is remarkably similar to that in second-growth forests in the southwestern portion of the reserve. Compared with old-growth forest, secondary forests present high abundances of frugivores, long-flight insectivores, and terrestrial granivores, and lower numbers of short-flight insectivores (Protomastro et al. 1990). As in our study area, the second-growth forests in the southwestern portion of the reserve also are characterized by a high density of thin stems in the shrub layer and a low density of trees (Protomastro et al. 1990). Therefore, we could infer that birds have a common response to structural changes that resemble edge-related conditions. In addition, several of the birds associated with our forest edge are opportunistic, early successional species characteristic of woodland edges or brushlands and commonly are regarded as "edge species" elsewhere in the Chaco region and in vastly different forests (e.g. *Tyrannus melancholicus, Coryphospingus cucullatus, Zonotrichia capensis, Turdus amaurochalinus*; Short 1975, Willis 1979, Scott and Brooke 1985).

Seasonal deciduous woodlands in South America are facing accelerating rates of degradation and fragmentation (Lerdau et al. 1991). In particular, Chaco semiarid forests could be considered conservation "hotspots" in South America (Beissinger et al. 1996). In Argentina, they have a long history of modification, fragmentation, and decline due to intense human exploitation and misguided management (Morello and Saravia Toledo 1959, Morello and Adamoli 1974, Short 1975, Bucher 1982, Aizen and Feinsinger 1994). These practices have increased the frequency of edge habitats. At the same time, selectively logged areas regenerate into second-growth forest like those studied in the reserve (Protomastro et al. 1990). Based on this evidence, and on the similarity of natural edges with other types of edges (e.g. fire-controlled edges), Lopez de Casenave et al. (1995) have suggested that structural features of natural edges will predominate in the landscape if these trends continue at present rates. If it is true that birds respond in a similar way to roughly similar structural changes, we expect that temporal modifications in bird assemblages of old-growth forests will be similar to the spatial contrasts that we found between forest interior and edge. More important, however, edge effects on birds in newly created edges could be more severe than those in older edges. Additional studies are needed to identify the similarities and differences between natural and anthropogenic edges, and to determine the extent to which our results apply to other areas of the Chaco forest.

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