



Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico

ALEJANDRO ESTRADA^{1,*}, PIERLUIGI CAMMARANO² and ROSAMOND COATES-ESTRADA¹

¹Estación de Biología 'Los Tuxtlas', Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 176, San Andrés Tuxtla, Veracruz, México; ²Dipartimento di Biologia, Università degli Studi di Milano, Milano, Italy; *Author for correspondence (fax: +52-294-24367; e-mail: estrada48@yahoo.com)

Received 28 July 1999; accepted in revised form 5 January 2000

Abstract. Fragmentation of the lowland tropical rain forest has resulted in loss of animal and plant species and isolation of remaining populations that puts them at risk. At Los Tuxtlas, Mexico, lowland rain forests are particularly diverse in the avian fauna they contain and while most of the forests have been fragmented by human activity, many of the fragments still harbor diverse assemblages of bird species. In these landscapes, linear strips of residual rain forest vegetation along streams as well as linear strips of vegetation fences (live fences) crossing the pastures might provide some connectivity to bird populations existed in forest fragments. We investigated bird species richness and relative abundance in one 6-km long section of live fences (LF) bordering a dirt road and in two 6-km long sections of residual forest vegetation along a river (MR) and one permanent stream (BS). We used point count procedures which resulted in the count of 2984 birds representing 133 species. At the LF site we detected 74% of the species, 72% at the BS site and 57% at the MR site. Only 38% of the species were common among sites. Neotropical migratory birds accounted for 34–41% of the species counted at all sites. While edge and open habitat birds accounted for 6–10% of the species and for 50% of the records at the three vegetation strips, about 90% of the species were forest birds. Distance to forest fragments and degree of disturbance of the vegetation seemed to negatively influence bird species presence at the BS and MR strips. Rarefaction analysis indicated that the LF strip was richer in species than the other two sites, but the occurrence of the three vegetation strips in the landscape seem to favor the presence of many more species. We discuss the value of these vegetation strips to birds as stepping stones in the fragmented landscape.

Key words: bird diversity, conservation, corridors, forest fragmentation, Los Tuxtlas, Mexico, tropical rain forests

Introduction

Tropical rain forest destruction and fragmentation has been a major cause of loss of biological diversity (Wilcox and Murphy 1985). Negative effects of these human induced changes on bird populations such as diminished size and local extinction of species may result from loss of natural habitat (Robbins et al. 1989; Johns 1991; Hagan et al. 1996), isolation from other appropriate habitat (MaClintock et al. 1977;

Urban et al. 1988; Estrada et al. 1997), and from edge effects (Turner 1996; Offerman et al. 1995).

Many tropical nations like Mexico no longer possess large undisturbed areas of lowland tropical rain forest. Instead, the remaining forests consist of scattered and isolated collections of fragments (Estrada and Coates-Estrada 1996). The tropical rain forest of Los Tuxtlas, in the southeastern portion of the state of Veracruz, Mexico, represents the most northern limit of the lowland rainforests on the American continent. Avian diversity in these forests is high with about 550 species reported (Winker 1997). Currently, the forest has been deeply altered with approximately 75% of the forest converted to pastures, another 20% exists as isolated forest fragments in the lowlands, and only 5% is still preserved as extensive forested areas but located at elevations >800 m a.s.l. (Estrada and Coates-Estrada 1996).

Initial surveys of bird populations in clusters of isolated forest fragments in the Los Tuxtlas lowlands reported negative effects of loss area and isolating distance on bird species richness and relative abundance, but indicated as well that the presence of these fragments has allowed the persistence of many bird species that would have otherwise disappeared in a completely deforested landscape (Estrada et al. 1997). With this knowledge at hand, it is imperative to assess the effectiveness of corridors, among other options (e.g. buffer zones), to ameliorate the negative effects of fragmentation.

While the general value of corridors for conservation has been questioned (Hudson 1991; Simberloff et al. 1992), other studies suggest that corridors of vegetation (human-made or remnants of the original vegetation along the sides of streams and rivers) may be important in facilitating animal movements in a fragmented landscape by providing the needed physical connectivity among isolated forests or by acting as stepping stones (Nohlgren and Gustaffson 1995; Hass 1995; Ruefenacht and Knight 1995; Estrada and Coates-Estrada 1996; Beier and Noss 1998).

At Los Tuxtlas, single planted rows of the tree *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) are used by farmers and ranchers to hold barbed wire. These live fences (LF) crisscross the pastureland and are important to local ranchers and farmers to delimit boundaries of the land and to enclose their cattle and/or crops. Because, the posts grow rapidly in height and produce moderately foliated crowns, single rows of these live fences resemble corridors of vegetation across the pasturelands (Estrada et al. 1997). Other less common corridors of vegetation in the lowland landscape are segments of residual rain forest vegetation along streams and rivers.

Preliminary surveys of birds conducted by us in live fences indicated the presence of significant numbers of forest bird species and individuals in these habitats (Estrada et al. 1997). However, the extent to which forest birds use LF and other types of linear strips of native vegetation in the fragmented tropical landscape still lacks sufficient documentation (Petit et al. 1989). Therefore we investigated bird species richness and relative abundance in one 6-km long section of LF bordering a dirt road and in

two 6-km long sections of residual forest vegetation along a river and one permanent stream. These three sinuous strips of vegetation cut across an area (32 km^2) occupied by pastures and by a cluster of forest fragments under investigation by us in the last 5 years (Figure 1). We report here the results of these surveys and hope to enrich our understanding of avian flexibility to transformation of their habitat by humans. This report and others published earlier (Estrada and Coates-Estrada, 1996; Estrada et al. 1993a, b, 1994, 1996, 1997, 1998, 1999) attempt to infer what kind of landscape scenarios and mosaics might sustain maximum diversity and minimum species loss.

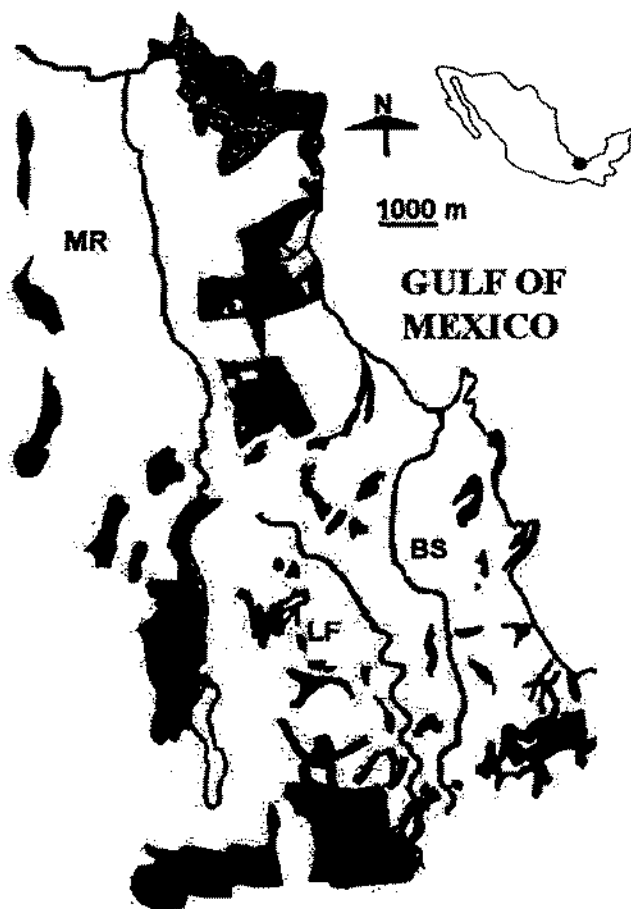


Figure 1. Study landscape in the region of Los Tuxtlas. The three strips of vegetation investigated are represented by the continuous lines (LF = live fence, BS = Balzapote stream, MR = Maquina river). Forest fragments shown in dark.

Methods

We conducted field work in the north-eastern area of Los Tuxtlas (95°00' W, 18°25' N; elevation sea level to 1600 m) in southern Veracruz, Mexico. Mean annual temperature is 27 °C and mean annual precipitation is 4964 mm (SD \pm 862, $N = 20$ years). Rainfall is distributed seasonally with the period March–May receiving an average monthly precipitation of 111 mm (\pm 11.7 mm) whereas average monthly precipitation the rest of the year is 486 mm (\pm 87.0 mm) (Estrada et al. 1985).

Study sites

The study sites were a 6 km section of a LF along the sides of a sinuous dirt road and two 6-km sections of residual forest vegetation along the edges of the Balzapote Stream (BS) and the Maquina River (MR) both flowing into the Gulf of Mexico. General orientation of the three sites was N to S following the altitudinal gradient from sea level to 160 m. The shortest linear distance separating the sites from one another were 250 m for the LF–MR sites, 500 m for the LF–BS sites and 2200 m for the BS–MR sites (Figure 1). Physically, the three corridors were an integral part of the fragmented local landscape occupied by pastures (10–15 cm high) and clusters of forest fragments ranging in size from 1 to 112 ha. Isolating distance among forest fragments (straight line distance to the edge of the nearest forest fragment) ranged from 0.2 to 0.8 km. The number of forest fragments present within a 250, 500 and 1000 m band on each of each corridor were, 10, 13 and 19 for the LF corridor, 7, 8 and 14 for the BS site and 1, 3 and 6 for the MR site (Table 1).

The vegetation of the LF site was mainly represented by live posts of *Bursera simaruba* and *Gliricidia sepium*, but other tree species (e.g. *Ficus* spp, *Cecropia obtusifolia*) established as a result of dispersal of seeds by birds and/or bats were occasionally present. The residual forest vegetation at the BS and MR sites was dominated by trees of the Lauraceae, Moraceae, Cecropiaceae, Boraginaceae and Leguminosae. However important differences were evident between the BS and MR sites in the degree of conservation of the vegetation with the latter site having a much more sparse tree vegetation. Both sites, however, had a few representatives of the forest palms *Astrocaryum mexicanum* and *Bactrix trichophylla* common in the understory of undisturbed forest vegetation in the region (Bongers et al. 1988) evidencing the residual nature of the vegetation found at these sites. At both the BS and MR sites cattle had access to the edge of the water and thus understorey vegetation was non-existent, except for the grazed pasture.

Bird counts

During 1997 one of us (PC) conducted visual counts of birds at the habitat investigated using the fixed-radius census points in a linear transect sampling procedure

Table 1. Results of bird counts at the sites investigated. Also shown are quantitative features of vegetation at each habitat (Mean \pm SD), number of forest fragments in the vicinity of each site, and the proportion of birds in each foraging guild at each site.

	Vegetation strip			Total
	Live fences	Balzapote stream	Maquina river	
Resident				
Species	58	63	49	73
Individuals	692	1226	606	2524
Migratory				
Species	40	33	27	56
Individuals	211	153	96	460
Total				
Species	98	96	76	133
Individuals	903	1379	702	2984
Tree species per plot	2.0 \pm 0.5	26.0 \pm 13.2	18.0 \pm 8.5	
dbh cm	15.0 \pm 0.4	33.0 \pm 12.5	47.0 \pm 18.2	
Canopy height m	6.3 \pm 2.7	15.8 \pm 3.5	16.9 \pm 2.6	
Forest fragments				
Within 250 m band	10	7	1	
Within 500 m band	13	8	3	
Within 1000 m band	19	14	6	
Foraging guilds				
	% Species	% Species	% Species	Average %
Aerial insectivore	33	34	29	32
Frugivore/insectivore	50	48	57	51
Granivore	7	4	3	5
Nectarivore	5	7	8	7
Carnivore	5	6	4	5

(Hutto et al. 1986), in which all perching individuals detected by sight within a 25 m radius of the point-count center were recorded. Each count lasted 5 min and at least 30 min elapsed between counts at each point. Count points were established at 150 m intervals for a total of 40 points per strip of vegetation.

We conducted all bird counts between 0630 and 1300 hrs, but 93% of our bird records at the three strips of vegetation were obtained between 0630 and 1000 hrs and avoided sampling in heavily overcast and rainy days. We sampled birds at each site 4 times, once in each quarter of the year and the average interval between samples ranged from 30 to 40 days. Birds counted were identified to species. Our records excluded those species detected flying across the landscape and well above canopy level. Crepuscular and nocturnal (e.g., Strigidae and Caprimulgidae) species were not recorded. Bird species counted were classified into five general foraging guilds according to components in their diet as reported in the literature (Coates-Estrada et al. 1993). Taxonomic nomenclature for birds followed the American Ornithologist's Union (1983).

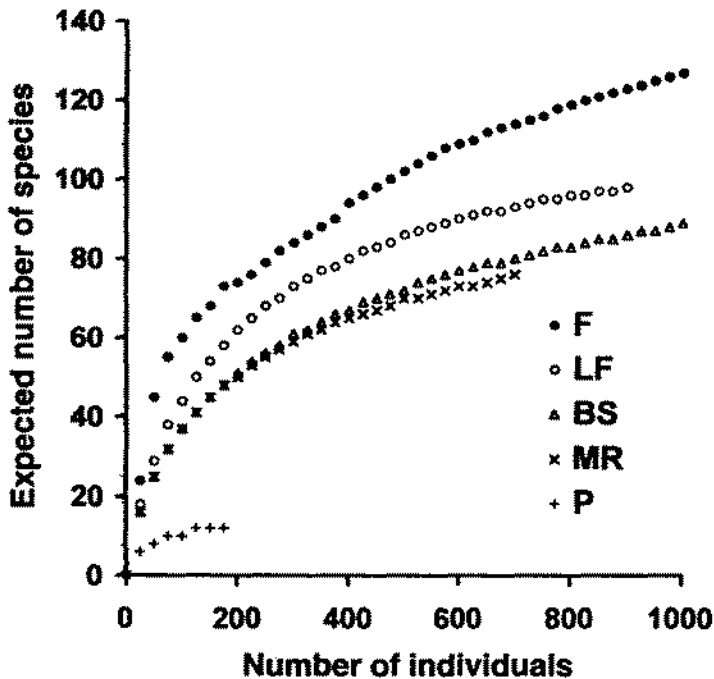


Figure 2. Rarefaction curves for the three vegetation strips investigated. Comparisons between sites made at $N = 500$. Data for forest fragments and pastures from another study (Estrada et al. 1997) in the same landscape is included for comparison. F = forests, LF = live fences, BS = Balzapote stream, MR = Maquina river, P = pastures. Note the high species richness of the live fence site and the species poor pastures.

records (Appendix). Neotropical migrant birds accounted for 42% of the species detected and for 15% of the birds counted in the total sample. The habitat with the highest proportion of Neotropical migrant bird species was the LF site (41%), followed by the MR (35%) and BS (34%) sites (Table 1). Seven species (*Dendroica magnolia*, *Icterus galbula*, *Vireo griseus*, *Wilsonia citrina*, *Setophaga ruticilla*, *Piranga rubra* and *W. pusilla*) accounted for 50% of the migrant counts at all sites and transient species (e.g., *Passerina cyanea*, *Tyrannus fortificatus*), accounted for 45% of Neotropical migratory species recorded (see Appendix).

Birds that depend on or complement their diet with fruit accounted for about 50% of the species while aerial insectivores made up 32% of the species. The distribution of foraging guilds was, in general, similar among the three corridors (Table 1). A general association was found between the bird's body mass (g) and the number of individuals counted per habitat ($r_s = 0.28$, $P = 0.001$, $N = 133$), but this association was weaker at the LF site ($r_s = 0.15$, $P = 0.001$, $N = 98$) than at the BS ($r_s = 0.41$, $P = 0.001$, $N = 96$) and MR ($r_s = 0.37$, $P = 0.001$, $N = 76$) sites, and no association existed between bird body mass and the number of sites in which species were present ($r_s = 0.12$, $P = 0.07$, $N = 133$).

Bird species in the LF site

In this habitat, we recorded the presence of 903 birds of 98 species. Five species, *M. aurifrons*, *P. sulfuratus*, *D. dives*, *C. morio* and *A. autumnalis*, accounted for 40% of the records and seven neotropical migrant species (*D. magnolia*, *V. griseus*, *W. pusilla*, *S. ruticilla*, *P. cyanea*, *I. galbula*, *Empidonax minimus*) contributed to 50% of the records for migratory species (see Appendix).

Bird species in the BS site

We recorded 1379 birds representing 96 species in the BS site. Seven species (*P. sulfuratus*, *D. dives*, *M. aurifrons*, *P. montezuma*, *C. morio*, *T. semifasciata* and *Bubulcus ibis*) accounted for 50% of the records (Appendix). Among the neotropical migrant species recorded at this site, six (*D. magnolia*, *I. galbula*, *W. citrina*, *Mniotilta varia*, *P. rubra* and *Empidonax traillii*) contributed to 50% of the records (see Appendix).

Bird species in the MR site

We counted 702 birds representing 76 species in the MR habitat. Eight species (*M. D. dives*, *A. autumnalis* and *Ramphastos sulfuratus*) accounted for slightly more than 50% of the records (Appendix). Neotropical migrant species such as *I. galbula*, *D. magnolia*, *W. citrina*, *Dendroica petechia*, *Tyrannus forficatus* and *E. minimus* contributed to 50% of the records for migratory birds (see Appendix).

Vegetation

Sites differed significantly in the vertical profile of the vegetation (Figure 3). The BS site had a higher density of vegetation than the MR site at all height intervals (Mann-Whitney *U*-test, $P = 0.02$) and the LF site differed significantly from the BS and MR sites in the same measure (Mann-Whitney *U*-tests, $P = 0.02$ in both cases). All three sites differed as well in mean tree dbh and in mean number of tree species per plot (Wilcoxon test, $P = 0.001$ in both cases). The lower tree species diversity per plot as well as the absence of cover at intermediate (0.5–3.0 m) vegetation height intervals was indicative of the higher degree of disturbance of the vegetation at the MR corridor compared to the BS site (Table 1).

Discussion

Our study showed that rich assemblages of bird species were present at the vegetation strips investigated. The resident bird species (e.g., *P. montezuma*, *C. morio*, *P. sulfuratus*) that numerically dominated the bird assemblages detected in these

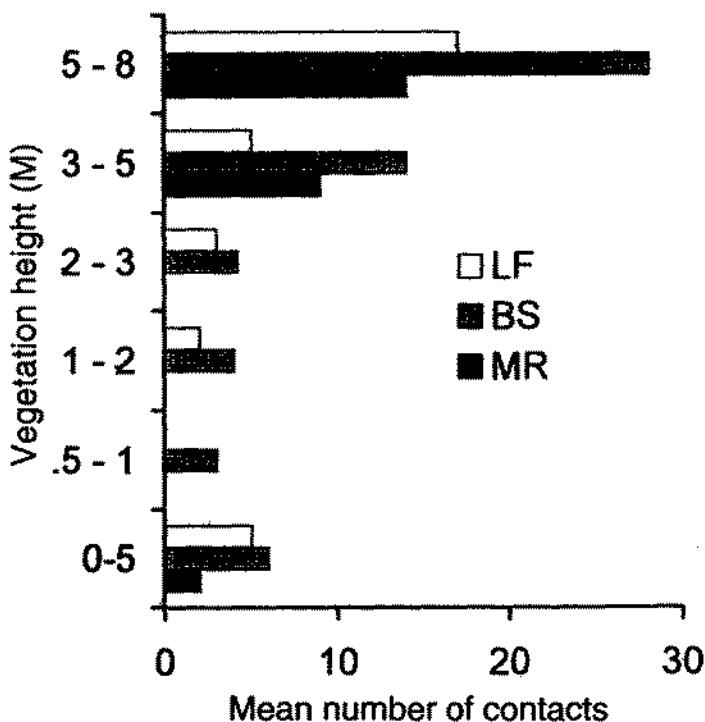


Figure 3. Vertical vegetation density profile for the three vegetation strips investigated. The BS strip had more plant cover at all height intervals, whereas the MR strip lacked plant cover at intermediate heights. The LF strip had the lowest density scores at each height interval.

habitats were typical of edge and open habitats (Stiles and Skutch 1989). It is possible that removal and fragmentation of the forest has resulted in more open and edge habitat available for dispersal and colonization by these bird species (Stiles and Skutch 1989). These species have a large body mass (60–380 g) and their gregarious mobbing behavior also allows them to displace smaller birds (body mass ranged for the rest of species recorded, excluding raptor and vultures, from 3 to 160 g) from perches and fruiting trees.

The abundance of *M. aurifrons* in the studied vegetation strips may be due to the presence of standing dead trees at the edges of nearby forest fragments and in the pastures where they may find supplies of wood boring insects. Some of these birds were observed also nesting at the BS and MR strips, probably the result of the greater aerial cover at this site. Likewise, the long distance mobility of species such as *A. autumnalis*, *R. sulphuratus* and *Pteroglossus torquatus* (Stiles and Skutch 1989), may allow them to visit greater numbers of forest fragments by using networks of vegetation strips in the local landscape to meet resource requirements and this may partly explain why they were common in our counts.

The fact that only from 45–47% of the total number of species counted were common among the studied sites suggests that the co-occurrence of the LF with the other two vegetation strips investigated seemed to favor the presence of more species ($N = 133$) in these sites as a group. Rarefaction analysis showed that the vegetation strips studied were significantly richer in bird species than pastures, suggesting that these habitats could be an important landscape element in the conservation of avian diversity preserved in forest fragments in the region. For example, 74% of the bird species detected in a sample of 50 forest fragments in the area were recorded at the three vegetation strips (Estrada et al. 1997).

While a few of the species (ca. 10%) detected at the vegetation strips were open and/or edge habitat specialists, about 45% were forest birds (e.g., *H. fuscicauda*, *Momotus momotus*, *Trogon violaceus*) and the rest were transient migratory birds (e.g., *T. fortificatus*, *Vireo flavifrons*, *Passerina ciris*) or winter residents (e.g. *Hyalocichla mustelina*, *Oporornis formosus*) that also require plant cover for protection and sustenance (Rappole 1995).

The LF site, in spite of its structural simplicity, as indicated by our vegetation measures, was particularly species rich (74% of all species detected). The LF and the BS sites were richer in species and more individuals were counted at these sites than at the MR habitat. These two sites also had more fragments in their vicinity than the MR site. The greater distance between the MR corridor and nearby forest fragments and the other two corridors as well as the sparser nature of the tree vegetation and lower foliage vertical density at the MR site, offering less protection to birds, may account for the lower number of species and birds recorded at this site. Nonetheless many bird species (56% of the total) were detected at this site.

Although the LF and the MR corridors, may not be suitable for sustained living because of the high exposure and disturbance of the vegetation, they might provide important services as stepping stones for a significant assemblage of resident and migratory bird species that differ in mobility, in general dietary habits and in general habitat requirements and that still exist in or visit the area (Estrada et al. 1997). Many of the birds observed perching in the vegetation strips studied flew toward nearby forest fragments or toward other LF strips. Vegetation strips such as the BS site with greater complexity of the residual forest vegetation than the MR site, may not only be used as a stepping stone, but also as a place of residency by some birds. For example, banded individuals of *H. fuscicauda* and *H. leucosticta*, were observed to reside in the same general location within the strip of vegetation throughout the year of field work (A. Estrada, unpublished).

Our study demonstrated that LF provide habitat for many bird species. The thousands of linear meters of vegetation in the form of LF across the pasturelands are available to birds inhabiting the fragmented landscape. Some of these LF may bring birds closer to nearby forest fragments thereby reducing isolating distances, may end at the edge of forest patches or may interconnect forest fragments with residual forest vegetation along streams and rivers, thus enhancing bird movements in

the area. For example, our records showed that even forest interior resident birds that rarely leave the forest such as *H. fuscicauda*, *H. leucosticta*, *B. culicivorus*, *M. momota* and *Euphonia hirundinaceae* were present at the LF site, suggesting the use of this habitat as an intermediate point when moving between nearby forest fragments.

The trees forming the LF not only provide temporary cover for birds, but also provide a rich set of micro habitats for insects. The LF trees also provide fruit, adding to the opportunities available to birds in a landscape where the forest is now a limited resource. However, LF may be unsuitable for prolonged residency by birds because of the exposure to raptors (e.g., *Buteo magnirostris*, *B. nitidus* during the day, owls at night) and other predators, including dogs and humans as well as exposure to extreme microclimatic conditions. This suggests that most of the birds counted in the LF site came from forest fragments in the vicinity.

Some LF possess high concentrations of plant species dispersed by birds and/or bats of the genera *Piper* (Piperaceae) *Solanum* (Solanaceae), *Cecropia* (Cecropiaceae), *Siparuna* (Mominaceae), *Eugenia* (Myrtaceae), *Psychotria* (Rubiaceae) and occasional strangler figs (*Ficus* spp.) and thus offer greater cover and the occurrence of abundant food supplies (large numbers of fruits produced per plant and year long availability) for fruit-eating specialists and for birds that complement their diet with important amounts of fruit (A. Estrada, unpublished).

While neotropical migrants comprised from 35% to 41% of all species counted at the studied sites, they comprised only an average of 21% (± 10.7) of the species counted at fifty forest fragments surrounding the investigated vegetation strips (A. Estrada, unpublished data), hence, stressing the importance of these strips to sustain local movements and in some cases to establish winter residency (Rappole 1995; Warkentin et al. 1995).

Our study suggests that the practice of using LF to section the pastureland seems to have unintentionally provided some degree of connectivity to isolated segments of populations of many bird species that differ in degree of mobility and that were isolated when the forest was fragmented (Estrada et al. 1997). The presence of thousands of LF of various lengths forming networks across the pastures lands where forest fragments are still preserved, coupled to the preservation of strips of residual forest vegetation along streams and rivers to preserve water and provide shade for cattle, as was the case for the BS and MR sites, may have helped, to this point, slow down the process of local disappearance of fragmented populations of bird species in certain landscapes of Los Tuxtlas.

It is evident that conservation of avian diversity under conditions of fragmentation in the lowlands of Los Tuxtlas, where contiguous forest has disappeared requires a landscape perspective. In this scenario, conservation of forest fragments is fundamental to preserve the indigenous biota, or at least a portion of it. However, conservation planning of isolated forest fragments is incomplete and consideration must be given to creating and sustaining connectivity (Neiman et al. 1993;

Turner 1996). Much of the controversy regarding the value of corridors revolves about whether or not animals other than edge species (ecological generalists) use corridors (Beier and Noss 1998). While our study showed that a few edge and open habitat bird species seemed to numerically dominate the bird populations in the investigated vegetation strips, it also showed that about 90% were bird species that prefer the forest interior and that both small and large species (excluding raptors and carrion feeders) and both resident and migratory species make use of these linear habitats.

In spite of the impressive diversity of bird species detected at the vegetation strips studied, it is necessary also to point out that not all species reported present (e.g. *Pipra mentalis*, *Crax rubra*, *Tinamus maior*, *Crypturellus boucardii*, *Spizaetus tyrannus* and *S. ornatus*) in a sample of fifty forest fragments in the same area where the vegetation strips are located (Estrada et al. 1997) were recorded during our counts, suggesting that these may be less resilient and are confined to the forest fragments where they reside.

While there is a cost (e.g., potential predation and higher time and energy expenditure) due to exposure and distances covered, bird species capable of reaching forest habitats outside of the patch in which they reside may encounter a greater variety of habitats in which to find resources and meet survival requirements. Such diversity of opportunities will increase significantly if a species can also make use of the human-made strips of vegetation available in the landscape (Pimentel et al. 1992). This could result in less concentration of mobile elements of the biota in the forest remnants, avoiding over exploitation of resources, increased competition and predation (Offerman et al. 1995). While large isolating distances may impose limits on the accessibility of these opportunities to birds, the use of LF and of vegetation along streams and rivers by birds as stepping stones may reduce isolation and ease crowding effects resulting from forest fragmentation (Harrison 1992; Lindenmayer and Nix 1993; Warkentin et al. 1995; Turner 1996; Estrada et al. 1997).

Although we agree with the recent tenet that corridors or the spatial configuration of remaining habitat can not compensate for the overall loss of habitat (Harrison and Bruna 1999), we believe also that we cannot ignore the high diversity of plant and animal organisms still present in fragmented tropical landscapes. Documentation of such biodiversity will provide information on the flexibility of response of species to disappearance and fragmentation of their habitat enhancing our biological data banks, and, for tropical nations where most of the contiguous forest has vanished, the conservation of fragmented landscapes may be the only option to preserve the remaining local and regional biodiversity.

Bearing this in mind, and that the generality of our results is limited because of the few sites sampled and the few sampling points in time, the study nevertheless suggests that in tropical regions, we need to identify land management practices (e.g. use of LF) that, already proven to work from the point of view of the farmer or rancher, seem to favor, by facilitating animal movements across the landscape, the persistence

of segments of the wildlife still preserved in existing forest fragments (Estrada et al. 1993b, 1994, 1997, 1998).

If the above scenario is conducive to preservation of important segments of wildlife in the forest fragments remaining in the landscape, efforts could be made toward improving its conservation value. For example, further investigation would be needed to distinguish between corridors that can support residency by birds (e.g. residual vegetation along streams and rivers with a high degree of vertical and horizontal complexity of the vegetation or LF with plant regrowth) versus corridors that facilitate bird movement (e.g. simple LF). In this case, aspects of design, such as width and connectivity to forest fragments as well as conservation of the understory vegetation, may deserve consideration (Saunders and de Rebeira 1991; Lindenmayer and Nix 1993; Beier and Noss 1998). Such an approach would make, as rightly pointed out by Turner and Corlett (1996), the task of conservation, technologically, economically and sociologically, easier, facilitating as well the potential restoration of the original ecosystem in the local fragmented landscape via the seed dispersal services of fruit-eating birds that visit the corridors (Estrada et al. 1993a; Guevara and Laborde 1993).

Acknowledgements

We thank the Lincoln Park Zoological Society and its Scott Fund for Neotropical Research for assistance to launch this research program and for its continued support, UNAM provided additional support.

Appendix. Bird species at the sites investigated ranked by total number of individuals counted. LF = live fence, BS, Balzapote stream, MR = Maquina river.

Species	Vegetation strip			Total	Average mass (g)
	LF	BS	MR		
<i>Melanerpes aurifrons</i>	68	157	71	296	80
<i>Pitangus sulphuratus</i>	65	154	69	288	60
<i>Dives dives</i>	64	152	38	254	150
<i>Cyanocorax morio</i>	59	73	60	192	285
<i>Psarocolius montezuma</i>	32	75	52	159	380
<i>Amazona autumnalis</i>	48	47	31	126	245
<i>Tityra semifasciata</i>	14	55	23	92	88
<i>Crotophaga sulcirostris</i>	36	30	22	88	82
<i>Dendroica magnolia</i>	34	23	12	69	9
<i>Columba flavirostris</i>	8	40	14	62	230
<i>Coragyps atratus</i>	18	39	1	58	1800
<i>Thraupis abbas</i>	8	32	17	57	40
<i>Bubulcus ibis</i>	2	45	7	54	340
<i>Buteo magnirostris</i>	6	28	19	53	350

Appendix. Continued.

Species	Vegetation strip				Average mass (g)
	LF	BS	MR	Total	
<i>Campylorhynchus zonatus</i>	24	21	7	52	30
<i>Ramphastos sulphuratus</i>	15	11	23	49	350
<i>Pteroglossus torquatus</i>	9	22	12	43	198
<i>Icterus galbula</i>	9	19	14	42	34
<i>Quiscalus mexicanus</i>	19	17	1	37	150
<i>Vireo griseus</i>	27	6	1	34	12
<i>Columbina inca</i>	14	19		33	52
<i>Wilsonia citrina</i>	6	18	9	33	11
<i>Tyrannus melancholicus</i>	9	11	12	32	40
<i>Turdus grayi</i>	4	8	19	31	72
<i>Amazilia candida</i>	9	12	7	28	4
<i>Setophaga ruticilla</i>	15	9	4	28	9
<i>Tityra inquisitor</i>	8	10	7	25	50
<i>Wilsonia pusilla</i>	16	5	4	25	7
<i>Aratinga nana</i>	2	16	6	24	85
<i>Chloroceryle americana</i>		10	13	23	35
<i>Piranga rubra</i>	8	13	2	23	30
<i>Saltator atriceps</i>	8	8	4	20	47
<i>Dryocopus lineatus</i>	7	10	3	20	169
<i>Empidonax minimus</i>	8	5	7	20	12
<i>Icterus cucullatus</i>	8	9	2	19	45
<i>Dendroica petechia</i>	5	3	9	17	8
<i>Euphonia hirundinacea</i>	6	9	2	17	27
<i>Dendroica virens</i>	5	6	5	16	9
<i>Myiarchus tuberculifer</i>	9	6		15	20
<i>Megarhynchus pitangua</i>	8	4	3	15	62
<i>Sporophila torqueola</i>	13	1	1	15	10
<i>Tyrannus forficatus</i>	5	2	7	14	45
<i>Myiodynastes maculatus</i>		7	6	13	40
<i>Habia fuscicauda</i>	4	6	3	13	46
<i>Myiozetetes similis</i>	4	7	2	13	45
<i>Passerina cyanea</i>	11	1		12	14
<i>Vireo gilvus</i>	4	5	3	12	12
<i>Basileuterus rufifrons</i>	12			12	18
<i>Anthracothorax prevostii</i>	2	3	6	11	6
<i>Columbina talpacoti</i>	9		1	10	48
<i>Thraupis episcopus</i>	2	6	2	10	35
<i>Campylopterus hemileucurus</i>	5	4	1	10	11
<i>Empidonax traillii</i>		9	1	10	13
<i>Trogon violaceus</i>		7	2	9	68
<i>Icteria virens</i>	5	1	2	8	25
<i>Polioptila caerulea</i>		6	2	8	6
<i>Sturnella magna</i>	8			8	75
<i>Mniotilta varia</i>	2		5	7	8
<i>Piranga olivacea</i>	5		2	7	28
<i>Buteogallus anthracinus</i>		2	5	7	800
<i>Sayornis nigricans</i>	4		3	7	18
<i>Myiarchus tyrannulus</i>	3	2	1	6	32

Appendix. Continued.

Species	Vegetation strip				Average mass (g)
	LF	BS	MR	Total	
<i>Myiodynastes luteiventris</i>	2	2	2	6	46
<i>Dumetella carolinensis</i>	2	3	1	6	37
<i>Pachyrhamphus aglaiae</i>		5	1	6	30
<i>Vireo flavifrons</i>	1		5	6	16
<i>Geothlypis poliocephala</i>	5	1		6	7
<i>Glaucidium brasilianum</i>		5		5	63
<i>Sayornis phoebe</i>	5			5	20
<i>Buteo nitidus</i>	2	3		5	500
<i>Momotus momota</i>	4	1		5	140
<i>Vermivora ruficapilla</i>	2	2	1	5	9
<i>Piranga ludoviciana</i>	2		3	5	25
<i>Ortalis vetula</i>		4		4	549
<i>Leptotila verreauxi</i>			4	4	165
<i>Amazilia tzacatl</i>	2	1	1	4	4
<i>Vermivora pinus</i>	2		2	4	9
<i>Columba nigrirostris</i>	1		3	4	162
<i>Thryothorus maculipectus</i>	3	1		4	14
<i>Troglodytes aedon</i>	4			4	10
<i>Henicorhina leucosticta</i>	3	1		4	16
<i>Parula americana</i>	3		1	4	8
<i>Seiurus noveboracensis</i>	2	2		4	17
<i>Geothlypis trichas</i>	1	3		4	12
<i>Cathartes aura</i>		4		4	1400
<i>Pyrocephalus rubinus</i>	4			4	17
<i>Tyrannus tyrannus</i>	3			3	40
<i>Polyborus plancus</i>	1	2		3	1000
<i>Piaya cayana</i>	1	2		3	105
<i>Phaethornis superciliosus</i>		2	1	3	6
<i>Contopus virens</i>		3		3	14
<i>Vireo solitarius</i>	2		1	3	17
<i>Protonotaria citrea</i>	2	1		3	15
<i>Habia rubica</i>		3		3	44
<i>Saltator coerulescens</i>			3	3	52
<i>Tiaris olivacea</i>	3			3	10
<i>Dendroica caerulescens</i>	3			3	9
<i>Lepidocolaptes souleyetii</i>		2		2	45
<i>Passerina ciris</i>	2			2	15
<i>Micrastur semitorquatus</i>	1		1	2	650
<i>Pionopsitta haematotis</i>			2	2	165
<i>Phaethornis longuemareus</i>	2			2	3
<i>Empidonax alnorum</i>		2		2	12
<i>Empidonax flaviventris</i>	1	1		2	11
<i>Catharus ustulatus</i>	2			2	31
<i>Hylocichla mustelina</i>	1	1		2	47
<i>Dendroica dominica</i>		2		2	9
<i>Euphonia affinis</i>		2		2	16
<i>Spiza americana</i>	2			2	28
<i>Herpetotheres cachinnans</i>	1			1	600

Appendix. Continued.

Species	Vegetation strip				Average mass (g)
	LF	BS	MR	Total	
<i>Archilocus colubris</i>			1	1	3
<i>Florisuga mellivora</i>		1		1	7
<i>Chloroceryle amazona</i>		1		1	110
<i>Automolus ochroaemus</i>	1			1	44
<i>Contopus sordidulus</i>		1		1	12
<i>Empidonax albigularis</i>		1		1	11
<i>Empidonax virescens</i>		1		1	12
<i>Empidonax</i> sp.			1	1	12
<i>Myiarchus crinitus</i>	1			1	34
<i>Catharus guttatus</i>		1		1	31
<i>Turdus migratorius</i>	1			1	79
<i>Dendroica castanea</i>		1		1	12
<i>Dendroica coronata</i>	1			1	12
<i>Dendroica palmarum</i>	1			1	10
<i>Dendroica pensylvanica</i>		1		1	10
<i>Seiurus motacilla</i>			1	1	16
<i>Oporornis formosus</i>	1			1	13
<i>Coereba flaveola</i>		1		1	12
<i>Piranga leucoptera</i>	1			1	15
<i>Pheucticus ludovicianus</i>	1			1	45
<i>Volatinia jacarina</i>		1		1	12
<i>Icterus mesomelas</i>		1		1	60
<i>Amblycercus holosericeus</i>		1		1	65
Species	98	96	72		
Individuals	903	1379	702	2984	

References

- American Ornithologists Union (1983) Check-list of North American Birds. American Ornithologist Union, Allen Press, Lawrence, Kansas
- Beier RI and Noss RF (1988) Do habitat corridors provide connectivity? *Conservation Biology* 6: 1241-1252
- Bongers F, Popma J, Meave del Castillo J and Carabias J (1988) Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55-80
- Estrada A and Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas. *International Journal of Primatology* 5: 759-783
- Estrada A, Coates-Estrada R and Martínez M (1985) La Estación de Biología 'Los Tuxtlas': un recurso para el estudio y conservación de las selvas del trópico húmedo en México. In: del Amo S and Gomez-Pompa A (eds) *Regeneración de selvas II*, pp 379-393. Editorial Alhambra Mexicana, S.A. de C.V. Mexico
- Estrada A, Coates-Estrada R, Merritt D Jr, Montiel S and Curiel D (1993a) Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. In: Fleming TH and Estrada A (eds) *Frugivores and Seed Dispersal: Ecological and Evolutionary Aspects*, pp 245-257. Kluwer Academic Publishers, Dordrecht, The Netherlands
- Estrada A, Coates-Estrada R and Merritt D Jr (1993b) Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16: 309-318

- Estrada A, Coates-Estrada R and Meritt D Jr (1994) Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* 17: 229-241
- Estrada A, Coates-Estrada R and Meritt DA Jr (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 6: 19-43
- Estrada A, Coates-Estrada R, Anzures DA and Cammarano P (1998) Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 14: 577-593
- Estrada A, Anzures DA and Coates-Estrada R (1999) Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology*
- Fitch R (1992) WinSTAT, The Statistics Program for Windows, Kalmia, Cambridge, Massachusetts
- Guevara S and Laborde L (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. In: Fleming TH and Estrada A (eds) *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*, pp 319-338. Kluwer Academic Publishers, Dordrecht, The Netherlands
- Hagan JM, Vander Haegen M and Mckinley PS (1996) The early development of forest fragmentation effects on birds. *Conservation Biology* 10: 188-202
- Harrison RL (1992) Toward a theory of inter-refuge corridor design. *Conservation Biology* 2: 293-295
- Harrison S and Bruna E (1999) Habitat fragmentation and large-scale conservation. What do we know for sure. *Ecography* 22: 5
- Hass C (1995) Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* 4: 845-854
- Hudson WE (ed) (1991) *Landscape Linkages and Biodiversity*. Island Press, New York
- Hutto RL, Pletschet SM and Hendricks P (1986) A fixed radius point count method for nonbreeding and breeding season use. *The Auk* 103: 593-602
- Johns AD (1991) Responses of amazonian forest birds to habitat modification. *Journal of Tropical Ecology* 7: 471-437
- Lindenmayer DB and Nix HA (1993) Ecological principles for the design of wildlife corridors. *Conservation Biology* 3: 627-630
- Ludwig JA and Reynolds JF (1988) *Statistical Ecology*, John Wiley and Sons, New York
- MacClintock L, Whitcomb RF and Whitcomb BL (1977) Island biogeography and habitat islands of eastern forest. II. Evidence for the value of corridors and minimization of isolation in the preservation of biotic diversity. *American Birds* 31: 6-12
- Neiman RJ, Decamps H and Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 2: 209-212
- Nohlgren E and Gustaffson L (1995) Vegetation corridors: a literature review with comments from a Swedish perspective. Report no. 1. Skogforsk, Upsala
- Offerman HL, Dale VN, Pearson SM, Bierregaard O Jr and O'Neill RV (1995) Effects of forest fragmentation on neotropical fauna: current research and data availability. *Environmental Review* 3: 190-211
- Petit DR, Petit JL and Smith HG (1989) Habitat associations of migratory birds overwintering in Belize, Central America. In: Hagan JM and Johnston DW (eds) *Ecology and Conservation of Neotropical Migrant Landbirds*, pp 247-256. Smithsonian Institution Press, Washington, DC
- Pimentel D, Stachow DA, Takacs HW, Brubaker AR, Dumas JJ, Meaney JAS, O'Neil D, Onsi E, Corzilius DB (1992) Conserving biological diversity in agricultural/forestry systems. *BioScience* 5: 354-362
- Rappole JH (1995) *The Ecology of Migrant Birds*. Smithsonian Institution Press, Washington, DC
- Robbins CS, Dowell BA, Dawson DK, Colon J, Estrada R, Sutton A, Sutton R and Weyer D (1989) Comparison of neotropical migrant land bird populations wintering in tropical forests, isolated forest fragments and agricultural habitats. In: Hagan III JM and Johnston DW (eds) *Ecology and Conservation of Neotropical Migrant Birds*, pp 207-220. Smithsonian Institution Press, Washington, DC
- Ruefenacht B and Knight RL (1995) Influences of corridor continuity and width on survival and movement of deer mice *Peromyscus maniculatus*. *Biological Conservation* 71: 269-274
- Saunders DA and de Rebeira CP (1991) Values of corridors to avian populations in a fragmented landscape. In: Saunders DA and Hobbs RJ (eds) *Nature Conservation 2: The Role of Corridors*, pp 221-240. Surrey, Beatty and Sons, Chipping Norton, Australia

- Schemske DW and Brokaw N (1981) Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938–945
- Simberloff D, Farr JA, Cox J and Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6: 493–505
- Stiles FG and Skutch AF (1989) A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York
- Turner IM (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33: 200–209
- Turner IM and Corlett RT (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. *Tree* 11: 330–333
- Urban DL, Shugart HH Jr, De Angelis DL and O'Neil RV (1988) Forest bird demography in a landscape mosaic. Publication no. 2853. Oak Ridge National Laboratory, Oak Ridge, Tennessee
- Wilcox BA and Murphy DD (1985) Conservation strategy: The effects of fragmentation on extinction. *American Naturalist* 125: 879–887
- Winker K (1997) Introduccion a las aves de Los Tuxtlas. In: Soriano EG, Dirzo R and Vogt RC (eds) *Historia Natural de Los Tuxtlas*, pp 534–556
- Warkentin IG, Greenberg R and Salgado Ortiz J (1995) Songbird use of gallery woodlands in recently cleared and older settled landscapes of Selva Lacandona, Chiapas, Mexico. *Conservation Biology* 5: 1095–1106