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Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico

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Faced with rapid and extensive conversion of tropical rain forests to a landscape consisting of pasture lands, and with the need to preserve the avian diversity of tropical regions, it is imperative to determine how different species have responded to anthropogenic alterations of their natural habitats. We sampled birds in undisturbed and disturbed forest islands in regenerating forests and in four replicates of each of the following man-made habitats: arboreal agricultural habitats (cacao, coffee, mixed, citrus and allspice), non-arboreal agricultural habitats (corn, jalapeño chili pepper and bananas), live fences and pastures, at Los Tuxtlas, Veracruz, Mexico. We censused 22 145 birds representing 226 species. We detected 79% of the species in forest habitats, 80% in agricultural habitats, 43% in live fences and only 5% in pastures. Isolating distance and continued disturbance by humans of forest fragments were important variables influencing species' richness. Arboreal agricultural habitats and live fences were richer in species and in birds than non-arboreal man-made habitats. Economic surveys showed that some of the crops investigated yield higher returns than cattle ranching based on pastures. We discuss the conservation value for birds of agricultural islands and of live fences as landscape elements that help reduce physical and biotic isolation among remaining configurations of forest fragments in Los Tuxtlas.

Keywords: tropical rain forest; Mexico; Los Tuxtlas; bird diversity; conservation.

Introduction

Faced with rapid and extensive conversion of tropical rain forests to a landscape consisting of pasture lands and with the need to preserve the remaining wildlife, it is imperative to determine how different species have responded to anthropogenic alterations of their natural habitats. Reports on which bird species have survived the destruction, fragmentation and isolation of tropical rain forests and how they are responding to such changes exist only for few localities in Central and South America (see Willis, 1974; Lovejoy *et al*., 1984, 1986; Karr, 1990; Johns, 1991). Data on Neotropical bird responses to the conversion of rain forest habitat to agricultural vegetation are almost non-existent (but see Robbins *et al*., 1987, 1989, for preliminary reports on neotropical migrants).

In the region of Los Tuxtlas, in southern Veracruz, Mexico, lowland tropical rain forests reach their northernmost distribution in the American continent and are notable for their high biological diversity (Pennington and Sarukhán, 1968; Estrada *et al*., 1985). However, land management practices have converted 80–90% of these forests to pastures for raising cattle. The remaining forests consist of collections of fragments of various sizes and with different histories of isolation which, together with fewer patches of regenerating forests, are found scattered throughout the region in a sea of pasturelands (Dirzo and Garcia, 1992; Estrada and Coates-Estrada, 1988).

In the landscape of Los Tuxtlas, agricultural activities occur sporadically in time and space in a 'sea' of pasture and occupy only about 3% of the land. These consist of cultivation of non-arboreal crops such as corn (*Zea mays*, Graminae), jalapeño chili pepper (*Capsicum* spp. Solanaceae), beans (*Phaseolus vulgaris*, Leguminosae), tobacco (*Nicotiana tabacum*, Solanaceae) and bananas (*Musa* spp). Cultivation of arboreal crops is also practiced. Of these, the most common are citrus (*Citrus sinensis*, Rutaceae), allspice (*Pimienta diocia*, Myrtaceae) and cacao (*Theobroma cacao*, Sterculiaceae). Farmers cultivate coffee (*Coffea arabica*, Rubiaceae) as a single crop. Less common is the cultivation of plots of mixed crops that include coffee and cacao. Rain forest trees left by farmers provide shade in the case of cacao, coffee and mixed plantations.

A common feature in the landscape of Los Tuxtlas are the live fences. It is a common practice among farmers and ranchers of Los Tuxtlas to use live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) to hold barbed-wire fences to divide the pasture land into smaller plots, to delimit the boundaries of their properties, and in some cases to rotate their cattle from one pasture plot to another. Because these posts grow rapidly in height and trunk diameter and produce moderately foliated crowns, single mature rows of these live fences resemble corridors of vegetation criss-crossing the pasture lands.

At Los Tuxtlas almost nothing is known about the effects of forest fragmentation on the avifauna (but see Rappole *et al.*, 1989; Robbins *et al.*, 1989; Winker *et al.*, 1990) and we also lack basic information on the conservation value of different types of land management subsystems that, in conjunction with the conservation of the remaining tropical rain forest fragments, can suggest ways of preserving species and sustaining local economies. Such information is fundamental for determining what remains of the original biological diversity, as represented by particular animal taxa, and for assessing the adaptive responses of animals to changes in the tropical rain forest landscape.

To contribute to the above, we present information in this paper on relative abundance and detection rates of bird species present in isolated rain forest fragments and in man-made vegetation representing eight types of agricultural crop. Data are also presented on bird species present in live fences and in pasture habitats. Results of surveys aimed at assessing the economic yield of the human made habitats studied are also presented.

Methods

We conducted field work in the North-eastern area of the region of Los Tuxtlas (95° 00′ W, 18° 25′ N; elevation sea level to 1600 m) in southern Veracruz, Mexico (Fig. 1). The mean annual temperature is 27°C and mean annual precipitation is 4964 mm (SD ± 862 N = 20 years) with a seasonal distribution (Estrada *et al.*, 1985). Birds were censused during 1990–1992 in 50 forest sites, in 32 agricultural habitats representing eight types of crop, in four live-fence sites and in four pasture sites. Sites ranged in elevation from sea level to about 800 m and were located in two zones within the study area, selected to have some control over spatial variation in distribution of the organisms under investigation (Fig. 1).

The 50 forest islands studied varied in isolating distance (distance to edge of the nearest forest fragment) (0.2–8.0 km). Area of forest fragments, obtained by digitizing aerial photos and by corroboration in the field, ranged from 1 to >2000 ha (Table 1). At each site we estimated time (years) since isolation (isolation = complete separation of forest from major forested land mass) by examining vegetation maps for the period before 1967, aerial photographs taken in 1967 and 1979, satellite images taken in 1986 and 1990 and by field surveys. Isolating age ranged from 5 to 35 years.

We sampled birds in four replicates in each of the following arboreal and perennial agricultural habitats: cacao, coffee, mixed crops, citrus and allspice. We sampled the same number of replicates for birds in the case of seasonal non-arboreal crops such as corn, jalapeño chili pepper, and bananas. Tall (>15 m) rain forest trees left by the farmers provided shade in the case of cacao, coffee, and mixed plantations. The agricultural plots ranged in size from 2 to 10 ha for a total accumulated area of 100 ha and coffee, cacao, mixed, citrus and allspice plantations ranged in age from 12 to 15 years; all habitats were fruit-productive. These habitats were isolated from other similar habitats and from forest habitats. Distance to the nearest forest fragment regardless of size ranged from 200 to 6000 m; distance to the nearest plantation ranged from 200 to 1000 m.

We censused birds in four live-fence sites about 2 km long each located across the pasture land and in the vicinity of the forest and agricultural habitats studied; each of these sites was at least 5 km away from the others. We also surveyed the avifauna in four areas of pasture, 25 ha each, totally devoid of the original forest vegetation and at least 5 km apart from each other, but within a 5 km radius of the forest sites we studied. In the pastures, we located the sampling area in the centre of each of the plots.

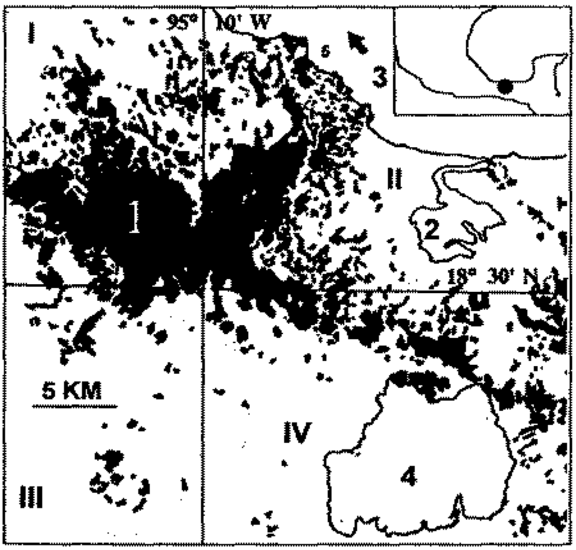

Figure 1. Northeastern section of the region of Los Tuxtlas in Southern Veracruz, Mexico. The remaining lowland rain forest is shown as dispersed fragments in black. The area was divided into four zones following longitude and latitude (95° 10' W–18° 30' N). Study sites (forests, agricultural habitats and live fences) were located in zones II and IV. The map has been drawn from satellite images taken in April 1990. 1 = San Martin Volcano (1600 m above sea level); 2 = Lake Sontecomapan; 3 = Gulf of Mexico; 4 = Lake Catemaco.

We conducted visual censuses of birds at the habitats investigated using existing trails or new trails opened by us and used the fixed-radius census point sampling procedure (Hutto *et al.*, 1986). Sampling points were established at 50–80 m intervals along trails. At the forest sites, the number of census points per site ranged from six (sites 1–5 ha) to 23 (sites 1000–2000 ha) (see Table 1 for the forest size classes and census points recorded). At the man-made habitats, 10 point-count locations, separated each by about 50 m and located along trails, were used to survey the avifauna. In total, 459 census points were completed for the 50 forest sites and 400 census points were completed for the 40 man-made habitats (Table 1).

Census routes were chosen to minimize trail overlap within and between days and thus the probability of viewing the same individual more than once. Census trails were at least 30 m from the edge of the vegetation patch under investigation. In all cases two observers walked the trails to census birds. Each point-count census lasted 5 min and at least 30 min elapsed between censuses at each point. Our records excluded those species detected flying across the landscape and well above canopy level. We conducted all counts between 0600 and 1200 (70% of samples) and between 1600 and 1800–1900 h (30% of samples) during 3 days at each site. Taxonomic nomenclature for birds followed the American Ornithologists' Union (1983). To control for seasonal variations in the presence and activity of birds, we sampled four replicates per man-made habitat in each quarter of the year for two annual cycles for a total of 320 samples. Samples for each forest site included one sample per each quarter of the year for a total of 200 samples (results of seasonal patterns in avian diversity will be presented elsewhere).

We quantified the vegetation at each site by recording all trees ≥10 cm in circumference at breast level and at least 1.5 m in height in six 10 m × 10 m plots. We located the plots randomly within the area where we sampled the birds; the plots were at least 30–40 m from each other. For each tree, we recorded the species (taxonomic nomenclature for plants follows Ibarra and Sinaca, 1987), maximum height and circumference. We measured vertical foliage density at four randomly selected spots within each of the six plots by scoring vegetation intercepts along a vertical pole at the following intervals: 0–0.5 m, 0.51–1.0 m, 1.1–2 m, 2.1–3 m, 3.1–5 m, 5.1–8 m, 8.1–10 m, 10.1–15m, >15 m (Schemske and Brokaw, 1981). We expressed intercepts at each height interval as the proportion of total intercepts recorded per site in each habitat and foliage vertical diversity using the Shannon-Weaver information index (H') (Ludwig and Reynolds, 1988). We expressed horizontal plant diversity per habitat as the mean number of tree species censused per site in each habitat. We divided the agricultural vegetation into shaded (cacao and coffee) and not shaded (citrus and allspice) and into arboreal (cacao, coffee, mixed, citrus, and allspice) and not arboreal (corn and jalapeño chilli pepper) for some descriptions and comparisons.

Because 15% of forest fragments studied represented different stages of conservation, regeneration and disturbance of the original vegetation, we selected, for comparison, four replicates of each of the following: disturbed forests (strong edge effect, hunting and selective removal of hardwoods, firewood and other), old second growths (regenerating forests 20–35 years old) and young second growths (5–15 years). Bird detection rates at these sites were compared to those of four undisturbed forests (isolated forest sites without further human intervention) selected at random from our data base.

We compared bird and species counts across vegetation types using mean number of birds and species observed per census point in each habitat (see Hutto *et al.*, 1986, for

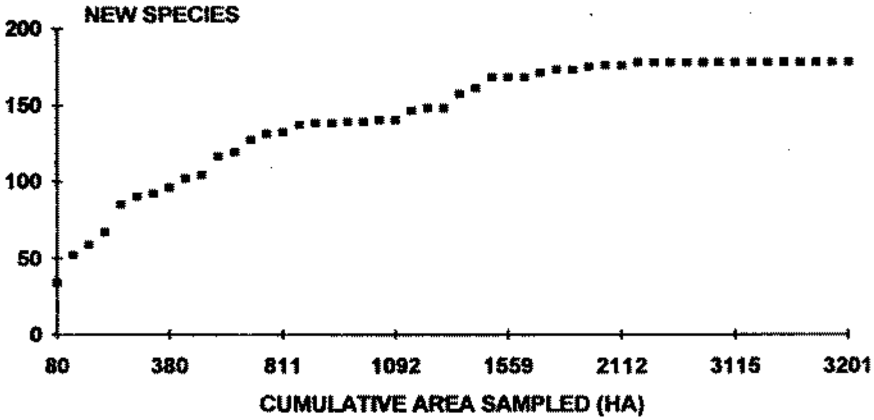

Figure 2. Cumulative number of bird species detected, and cumulative area sampled.

assumptions and biases of this method) and used rarefaction as an alternative to species richness indices to compare species richness among habitats where sample sizes differed (James and Rathburn, 1981). We used the dissimilarity index (PD) and the polar ordination procedures of Bray-Curtis (Ludwig and Reynolds, 1988) to measure the degree of resemblance when comparing forests and man-made habitats in species assemblages. We used Spearman rank correlation, partial correlation analysis and the Wilcoxon test when comparing variables and means between groups (Ludwig and Reynolds, 1988; Fitch, 1992). Since Neotropical migrant birds may be less responsive to some of the biogeographical variables examined in forest fragments (isolating distance, age of isolation and area), we calculated Spearman rank correlation on data for resident birds only when examining the effects of such variables. Means and standard deviations are given throughout the paper.

We conducted economic surveys in five private ranches and five communal farms ('ejidos') to determine the average number of cattle heads sustained per hectare and the selling price of standing beef. We also monitored revenues from milk production sold to the Nestle company and incorporated these into a gross estimate of the total revenues per hectare per year provided by cattle ranching. In the case of the plantations we interviewed the owners of the parcels to determine the productivity of the cash crop (kg ha^{-1}) and monitored the selling prices of the cash crops in the region over 3 years to grossly estimate average earnings on a per hectare per year basis. The number of man/days invested in the field for each agricultural activity and for cattle ranching were calculated from our surveys.

Results

General aspects

We censused 22 145 birds representing 226 species. Of the species censused, 79% were found in forest habitats, 80% in agricultural habitats, 43% in live fences and only 5% in the pastures. Of the individuals censused, 22% were counted in forest fragments, 58% in agricultural habitats, 17% in live fences and only 3% in pastures (Table 1). Because the cumulative species curve in the forest sites tended to level off after 1800 ha (30 sites), we feel that our sample provides a reasonably good representation of the species present in the

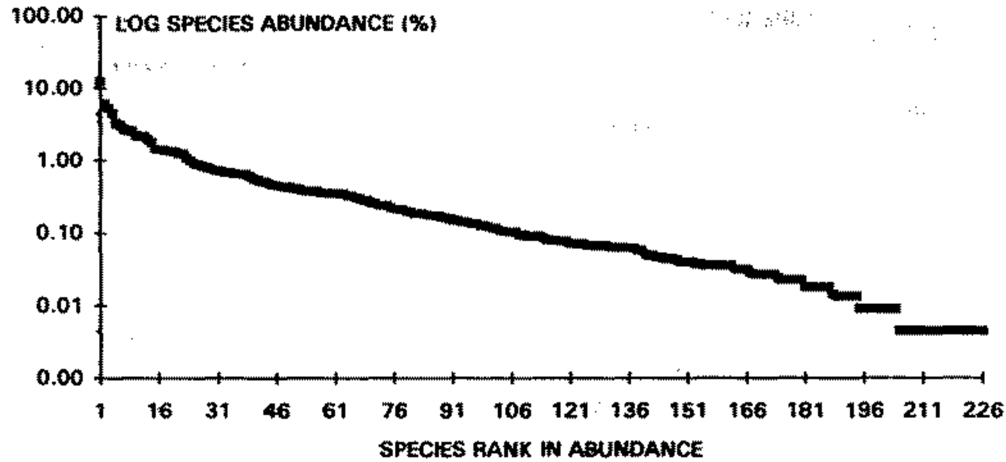

Figure 3. Dominance diversity curve for the bird community detected. Note the asymmetry of the curve and the relatively high dominance of first 10 species.

forest remnants in the study area (Fig. 2). In the total sample, 12 species accounted for 50% of all bird records, but 94% contributed to ≤1% of the records (Fig. 3 and Appendix 1). Four species, *Dives dives*, *Cyanocorax morio*, *Melanerpes aurifrons* and *Quiscalus mexicanus* accounted for 30% of the records, but these species were significantly more common in non forest than in forest habitats (see below and Appendix 1).

Neotropical migrant birds accounted for 30% of the species detected and for 18% of the birds censused. Of the neotropical migrants, 87% were censused in the Jan–March (49%) and Oct–Dec (38%) periods. No migrants were recorded in June and the earliest species arrival recorded in July was represented by *Seiurus motacilla*. The top ranking species in the forest habitats were *Wilsonia citrina* and *Hylocichla mustelina* which accounted for 24% of the records. Species such as *Dendroica. magnolia*, *W. citrina*, *W. pusilla*, *Setophaga ruticilla* and *V. griseus* predominated in the arboreal agricultural and live fence habitats. In the non arboreal man-made habitats species such as *Passerina cyanea*, *Spiza americana* and *Dendroica coronata* were particularly common (Appendix 1).

Bird species in undisturbed forest fragments

We censused 4932 birds representing 178 species in the forest fragments; 15 species accounted for 50% of the records. Each of the rest of the species contributed to 1% or less of the detections. The mean number of bird species detected per census point in the forest sites was 4.9 ±2.9 (range 0.36–11.2) and mean number of birds counted per census point was 15.5 ±12.8) (range 0.44–68.0) (Table 1). On average, forest sites had 50% of the species in common. The two most common species in the censuses were *Habia fuscicauda* and *Henicorhina leucosticta* that contributed 15% of the records (Appendix 1).

Area, isolating distance and age of undisturbed forest fragments and richness of bird species

We found no relationship between species' richness and area of forest fragments ($r_s = 0.071$ ns; $n = 50$), but detected a significant negative relationship between site species' richness and isolating distance of forest fragments ($r_s = -0.616$, $p < 0.02$; $n = 50$) and between this latter variable and mean number of birds censused per census point per site

Table 1. Species and birds censused at the habitats investigated.

Habitat	Number of sites	Number of census points	Species	(%)	Mean number of species per census point	*n*	(%)	Mean number of birds per census point
Forest	50	459	178	79	4.9 + 2.9	4932	22	15.5 + 12.8
Cacao	4	40	123	54	4.8 + 1.0	2036	9	50.9 + 13.2
Coffee	4	40	98	43	4.2 + 1.6	1678	8	41.9 + 3.4
Mixed	4	40	86	38	3.8 + 0.7	2464	11	61.6 + 8.0
Citrus	4	40	82	36	3.8 + 1.0	2029	9	50.7 + 7.1
Allspice	4	40	65	29	3.0 + 0.7	1499	7	37.4 + 17.5
Live fence	4	40	97	43	4.6 + 1.6	3722	17	93.0 + 2.4
Jalapeño	4	40	21	9	1.2 + 0.2	780	4	19.5 + 4.4
Corn	4	40	31	14	1.2 + 0.9	2152	10	53.8 + 6.3
Bananas	4	40	9	4	0.5 + 0.2	160	1	4.2 + 0.1
Pasture	4	40	12	5	0.5 + 0.2	693	3	17.3 + 13.5
Total	90		226			22 145		

Forest size classes: 1–5 ha, $n = 6$ (34 census points); 10–20 ha, $n = 6$ (40 census points); 30–50 ha, $n = 4$ (45 census points); 60–80 ha, $n = 4$ (50 census points); 100–200 ha, $n = 9$ (60 census points); 300–400 ha, $n = 9$ (65 census points); 600–800 ha, $n = 8$ (75 census points); >1000 ha, $n = 4$ (90 census points). Numbers in parenthesis are species and individual mean (+ SD) detection rates per site in each habitat.

($r_s = -0.505$, $p < 0.02$; $n = 50$) (Fig. 4). Species' richness and the mean number of birds counted per census point per site were found associated to isolating age of forest fragment ($r_s = 0.348$, $p = 0.007$; $r_s = 0.378$; $p = 0.003$; $n = 50$). However, partial correlation analysis showed that when age of forest patch was held constant, both species' richness and mean number of birds censused per census point per site were only correlated with isolating distance (species' richness $r_{xy} = -0.85$, $p < 0.001$, $r_{xz} = -0.05$ ns; birds $r_{xy} = -0.37$, $p = 0.004$, $r_{xz} = -0.05$ ns).

Comparison of birds in undisturbed and disturbed forests and in second growth habitats

We detected a significantly higher mean number of bird species and birds per census point in undisturbed than in disturbed forests (Table 2). Young and old second growth were significantly richer in species and in birds detected per census point than the undisturbed and disturbed forest sites (Table 2). Young and old second growths did not differ in the mean number of species and birds detected per census point (Table 2).

Bird species' richness in pastures

Our surveys in the four pasture sites resulted in the census of 693 birds of 12 species. Two species, *D. dives* and *Sturnella magna*, accounted for 89% of the records; raptors (e.g. *Falco sparverius*, *Herpetotheres cachinnans*) accounted for 42% of the species censused at these habitats (Appendix 1). Detection rates of bird species per census point in pastures were among the lowest (0.50 ±0.2 species per census point) (Table 1).

Birds in agricultural habitats

We censused 13491 birds representing 180 species in the agricultural habitats (all man-made habitats, except live fences and pastures). Forty-eight species were recorded in these

Table 2. Mean detection rates of species and birds in four types of forest habitat (results of Wilcoxon test are shown below the table)

Habitat (4 sites and 20 census points per habitat)	Mean (± SD) number of species per census point	Mean (± SD) number of birds per census point
Undisturbed (uf)	1.80 ± 0.4	4.8 ± 1.9
Disturbed (df)	1.33 ± 0.5	3.1 ± 1.1
Young growth (yg)	2.27 ± 0.5	6.9 ± 4.0
Old growth (og)	1.89 ± 0.5	7.4 ± 4.6

Species: uf-df, $z = -1.92$, $p = 0.02$; uf-yg, $z = -2.13$, $p = 0.01$; uf-og, $z = -1.05$, $p = 0.29$; df-yg, $z = -2.74$, $p = 0.003$; df-og, $z = -1.47$, $p = 0.05$; yg-og, $z = -1.01$, $p = 0.15$. Individuals: uf-df, $z = -2.55$, $p = 0.01$; uf-yg, $z = -1.64$, $p = 0.04$; uf-og, $z = -1.68$, $p = 0.04$; df-yg, $z = -2.43$, $p = 0.01$; df-og, $z = -1.68$, $p = 0.04$; yg-og, $z = -0.42$, $p = 0.33$

habitats only. In the arboreal habitats we recorded 9706 birds representing 170 species. Mean number of bird species detected per census point in each habitat ranged from 3.0 ±0.7 (allspice) to 4.8 ±1.0 (cacao), and the mean number of birds counted per census point in each habitat ranged from 37.4 (allspice) to 61.6 (mixed plantation) (Table 1). These habitats had, on average, 33% of the bird species in common (Appendix 1). In these agricultural habitats 22 species (13% of total recorded at these sites) numerically dominated (>100 individuals each) the sample accounting for 66% of the records. Species such as *C. morio*, *D. dives*, *M. aurifrons*, and *Tytira semifasciata* accounted for 33% of the birds censused, but present also in this group were forest understory species such as *H. fuscicauda* and *H. leucosticta* (Appendix 1). We found no differences between shaded (cacao, coffee and mixed crops) and unshaded habitats (allspice and citrus) in the mean number of species and individuals detected per census point ($z = 1.78$, $p = 0.17$) ($z = 1.09$, $p = 0.47$).

In the non-arboreal habitats (jalapeño, corn and bananas), we censused 3092 birds of 43 species. Mean number of species detected per census point ranged from 0.50 ±0.5 (bananas) to 1.2 + 0.9 (corn) and mean number of birds censused per census point ranged from 4.0 (bananas) to 53.8 (corn) (Table 1). In these habitats, *D. dives* dominated the sample accounting for 37% of the records (Table 2). The rest of the species accounted for ≤5% of the records. These habitats had, on average, 42% of the species in common (Appendix 1).

Species detection rates and bird detection rates per habitat differed significantly between arboreal (cacao, coffee and mixed plantation) and non arboreal habitats (jalapeño, bananas and corn) (species: arboreal $\overline{X} = 3.92 \pm 0.6$, non-arboreal $\overline{X} = 0.96 \pm 0.4$; $z = -1.82$, $p = 0.03$; birds: arboreal $\overline{X} = 58.5 \pm 1.5$, non-arboreal $\overline{X} = 25.8 \pm 6.7$; $z = -1.92$, $p = 0.05$).

Birds in live fences

We recorded in these habitats 3722 birds of 97 species. Mean number of species detected per census point was 4.6 (range 2.4–6.7) and mean number of birds censused per census point was 93.05 (range 89.6–94.9) (Table 1, Appendix 1). Ten species accounted for 50% of the records. Among these were edge and open habitat species such as *D. dives* and *Crotophaga sulcirostris*, forest species such as *H. fuscicauda* and *Basileuterus culicivorus*, and Neotropical migrants such as *Wilsonia pusilla*, *Vireo griseus* and *Dendroica magnolia* (Appendix 1).

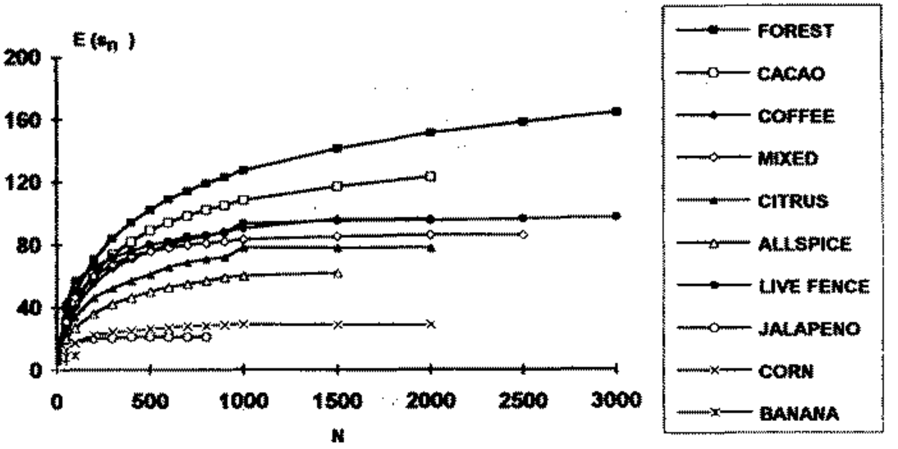

Figure 4. Rarefaction curves for all habitats examined. $E(s_n)$ is the expected number of species in a random sample of size n where s is the sum of the probabilities that each species will be included in the sample. Comparisons can be made of the expected number of species at different sample sizes. Comparison made at $n = 1000$.

Vegetation types used by bird species

We recorded 37 species only in forest habitats and 48 only in man-made habitats. We detected 72% of the species in our sample in both forests and in non-forest habitats (Appendix 1). Only *D. dives* and *M. aurifrons* were recorded in both forest habitats and in the 10 man-made vegetation habitats studied; 20% were present in six to eight man-made habitats in addition to the forests; 47% were present in forests and in two to five agricultural habitats (Appendix 1). We found no correlation between the number of vegetation types in which a species occurred and the species' mean body weight ($r_s = -0.07$ ns), but an association existed between the number of habitats in which a species was present and the rank order of individuals censused per species ($r_s = 0.840$, $p < 0.05$).

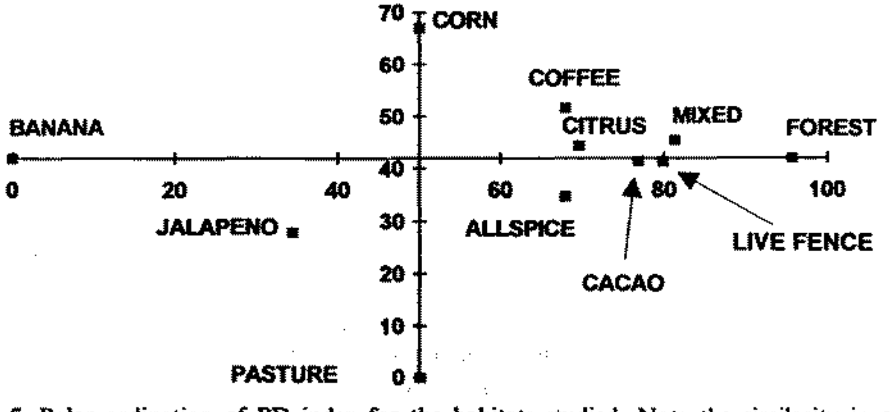

Figure 5. Polar ordination of PD index for the habitats studied. Note the similarity in species assemblages of live fences and of the arboreal agricultural habitats to the forests.

Forests and man-made habitats

Rarefaction curves showed that pastures followed by non-arboreal crops (jalapeño, corn and bananas) were the poorest habitats in species when sample size was controlled for. The analysis also showed that, at $n = 1000$, the most diverse habitats were the forests, followed by cacao, coffee, live fence, mixed, citrus and allspice (Fig. 4). Forests and agricultural habitats excluding pastures had 58% of the species censused at these habitats ($n = 224$) in common. In contrast, pastures had only 4% of the species in common with forest habitats and only 5% in common with agricultural habitats (Appendix 1). Polar ordination showed that the mixed and cacao plantations and live fence, were the habitats most similar to forest fragments in species assemblages. These habitats were followed by citrus, coffee and allspice. The least similar were the non-arboreal crops and pastures. These were also dissimilar with respect to each other (Fig. 5).

An examination of the vegetation data showed that the mean number of tree species censused per site in each habitat (MNTSH) and foliage vertical diversity per site habitat (FH′) were strongly correlated ($r_s = 0.97$, $p = 0.001$), with the forests and the three shaded man-made habitats being the most complex habitats. A similar analysis showed the mean number of bird species recorded per census point in each habitat (MSSH) significantly correlated with FH′ and MNTSH ($r_s = 0.67$, $p = 0.01$, $r_s = 0.72$, $p = 0.006$). Partial correlation analysis showed, however, that when the influence of MNTSH and FH″ were separately kept constant, MSSH and the mean number of birds per census point (MBSH) were significantly correlated only with FH′ (MSSH $r = 0.87$, $p < 0.001$; MBSH $r = 0.53$, $p = 0.04$).

Economic yield of the agricultural habitats studied

The gross estimates of our economic surveys indicated that some of crops studied produce higher economic benefits than cattle ranching (Table 3). Cacao, allspice and mixed plantations seemed to be highly productive options of land management with an average yield of US$2346.00 per hectare per year. Non-arboreal crops such as jalapeño and bananas also seemed to return high yields. One of the major differences between cattle ranching and the above-mentioned crops is the number of man/days required in the field to operate the crop. For example, the arboreal crops as a group required an average of 62 man/days in the field to operate with a range of 50 days (citrus) to 75 days (cacao). Cattle ranching, in contrast, requires an average of 40 days. Some of the non-arboreal crops investigated were very labour intensive, as was the case of jalapeño and bananas (Table 3).

Discussion

Our study showed the existence of a rich pool of forest bird species still existing in the fragmented landscape of Los Tuxtlas (60–70% of the species historically reported; Coates-Estrada *et al.*, 1985), but the majority of the species are present in low numbers. Our data also indicated that disappearance of the forest results in a great loss of bird species as attested by the near total absence of forest birds in the pasture habitats investigated. Data also showed that, although the number of birds occurring at the fragment may remain relatively unchanged, the outcome of continued human disturbance in these habitats is significant reductions in the number of existing forest bird species (see Johns, 1991, for similar findings in the Amazon basin).

Table 3. Gross estimates of average economic benefits, in US dollars per hectare per year, of land management practices at Los Tuxtlas

Land management	Man-days	kg ha^{-1}	Value (US$) kg^{-1}	Value (US$) per ha per year
Pasture land: cattle ranching (beef + milk)	40	1 head ha^{-1}	2.00	1650
Agricultural activity				
Cacao	75	500	6.00	3000
Coffee	65	600	2.30	1380
Citrus	50	6500	0.02	130
Allspice	70	500	5.00	2500
Mixed crops:				
Cocoa 0.5 ha		425	6.00	2550
Coffee 0.5 ha		400	2.30	920
Jalapeño	120	2500	1.00	2500
Bananas[a]	60	200 000	0.20	40 000
Corn	30	3000	0.23	690

[a]Banana plantations are very rare in Los Tuxtlas. Those investigated were operated by wealthy private ranchers or farmers.

Regenerating forests seemed to attract large numbers of birds. The density of the vegetation along vertical and horizontal dimensions as well as the presence of many fruiting tree species (e.g. *Cecropia obtusifolia* (Moraceae), *Ficus* spp. (Moraceae), *Stemmadenia donnell-smithii* (Apocynaceae), the presence of army ant swarms (*Eciton burchelli, Labidus praedator*), and the presence of a diverse fauna of insects and small vertebrates (lizards, amphibians) at these habitats (AE/RCE unpublished data) means the existence of protective cover and food resources for opportunistic frugivorous and insectivorous birds living there or visiting these habitats (Terborgh and Weske, 1969). If left alone, these forests may be an important conservation component in conjunction with the preservation of undisturbed forest fragments.

Pastures were a habitat particularly poor in bird species compared to the other habitats investigated. The near total absence of forest birds in pastures (we observed forest birds in pastures but flying overhead (>20 m) toward scattered groups of forest fragments) suggests that these are unsuitable habitats for them. Even species such as *D. dives*, that numerically dominated our sample in pastures, was more common in the man-made non-pasture habitats investigated. Lack of food resources, the extreme climatic conditions of pastures and the greater exposure of small birds to raptors in these habitats would make them inappropriate for continued bird habitation. We observed raptors such as *Buteo magnirostris, Falco sparverius, F. peregrinus* and *H. cachinnans* chasing and preying on small birds as these flew out of forest fragments into the pasture, suggesting that exposure to predators may be greater at the edge of the forest patch and out in the open pasture fields.

While there is a cost (e.g. potential predation and higher time and energy expenditure due to exposure and the 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 man-made islands of vegetation available in the landscape. 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 (Walker, 1981; Lovejoy *et al.*, 1986, Karr, 1990). However, isolating distance may impose limits on the accessibility of these opportunities for birds. In this instance, the use of small forest patches and of agricultural islands by birds as stepping stones may reduce isolation and ease crowding effects resulting from forest fragmentation.

Mist net data indicated that birds moved between forest patches and between forests and agricultural islands in the landscape (A.E. unpublished data), the use of all the habitats examined seemingly applied only to two of the species detected, *D. dives* and *M. aurifrons*; the rest are less resilient. At the other extreme were 37 species such as *Tinamou major*, *Crax rubra*, *Spizaetus tyrannus*, *S. ornatus* that occurred in forest habitats only (Appendix 1). Equally important is the observation that about 70% of the species detected were present in at least one habitat other than rain forest, suggesting the existence of variable plasticity among bird species and the possibility that some of these may be able to sustain their numbers as a result of their capacity to access a greater diversity of opportunities in the landscape.

The greater diversity of the vegetation along vertical and horizontal dimensions at the arboreal habitats possibly allows more bird species to co-occur at these sites. In contrast, habitats such as jalapeño chili pepper and corn are sporadic in time and space as a result of their seasonal appearance. After the harvest the fields are returned to pasture land; thus, these habitats are available to only those birds that use them for a few months in the year. In the banana plantations, the wide inter-row space and the sparse and non-woody nature of the stem and leaves of the plant mean lack of suitable perching sites and cover to birds. Only edge and open area birds, with generalist feeding habits and large body mass, such as *D. dives* and *O. mexicanus* (Stiles and Skutch, 1989), predominated at the non-arboreal man-made habitats. These birds will chase smaller birds from perching and feeding sites, thus diminishing the chances for bird visitation at these relatively open habitats (A.E. personal observations). Another important consideration is the heavy use of toxic pesticides in jalapeño chili pepper and corn habitats; such use is almost non-existent in the case of the other agricultural habitats studied.

While some man-made habitats were richer than others in bird species assemblages, it was the additive effect of bird species presence in several distinct habitats that resulted in high numbers of species recorded by us. All man-made habitats, excluding pastures, accumulated a total of 188 bird species, but singly, the mean number of species detected per habitat was 68 (range 9–123). Thus, the presence of these habitats in the landscape may compensate in part not only the loss of area of vegetation for birds, but also the lost heterogeneity of the landscape when the forest was converted to pasture. This situation may allow remaining mobile forest bird species that differ in ecological requirements to persist longer in time and space than if such heterogeneous collection of human-made habitats were not existing (Johns, 1991). Changes in land management practices in which pastures replace arboreal crops as a result of changes in commercial demands may have, like disappearance of the forest, important consequences for bird sustenance.

Hence, at Los Tuxtlas, we have bird species that can successfully occupy a variety of man-made habitats. At the other extreme are species that display intolerance and exist in a truly fragmented landscape. The majority of the species, however, seem to fall between these extremes. In this instance, a variegated model rather than a fragmentation model may be more adequate as a conservation approach at the landscape level (McIntyre and Barret, 1992).

At Los Tuxtlas, the conservation value for birds of arboreal agricultural islands as stepping stones could be enhanced by the presence of live fences. Our study showed that these habitats are intensively visited by a significant number of bird species (43% of the species detected in the total sample) living in the fragmented landscape. In this assemblage, 93% of the species were forest-interior birds. In contrast to the rectangular or square shape of agricultural habitats, the hundreds or thousands of linear metres of vegetation in the form of live fences across the landscape are available to birds inhabiting the many forest fragments in the region. Some of these live fences end at the edge of forest patches or interconnect with the forest vegetation remaining along streams and rivers, thus enhancing biotic connectivity in the area. For example, our records of forest birds such as *H. fuscicauda*, *H. leucosticta*, *B. culicivorus*, and *Euphonia hirundinaceae* in live fences are from those live fence sites that ended at the edge of a forest patch.

The trees forming the live fences not only provide cover for birds, but also constitute a rich set of micro habitats in which insects become established. The live fence tree (*Bursera simaruba*) also fruit in the year, adding to the opportunities available to birds in a landscape where now the forest is a limited resource. In those live fences where the vegetation has been allowed to regenerate under the trees, the presence of high concentrations of plant species of the genera *Piper* (Piperaceae) *Solanum* (Solanaceae), *Cecropia*, *Siparuna* (Mominaceae), *Eugenia* (Myrtaceae), *Psychotria* (Rubiaceae) and occasional strangler figs (*Ficus* spp.) suggests 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. Allowing the vegetation to grow under the posts may be a favourable strategy to maximize the number of species and of birds visiting these sites.

Our observations and interviews with the farmers indicated that very few of the birds detected in the agricultural habitats studies feed on the economically important fruits, and the damage these birds cause to the crops is insignificant. Instead, they seem to feed on insects living in the arboreal structures and on the ground (A.E. personal observation). It is likely that birds may contribute in important ways to the regulation of insect populations that are the major damaging agents of the plant's foliar and fruit parts in the plantations. Although many species use the agricultural habitats studied and the live fences for cover and possibly food at certain times of the year, lack of sufficient field data limits our knowledge as to whether they can support birds on a year-round basis. Predation rates or absence of preferred food resources or of tree cavities may make agricultural habitats and live fences unsuitable nesting environments for many other species as well.

Our economic surveys showed that, in contrast to cattle ranching, the cultivation of some of the crops studied may be a more economically productive mode of managing tropical land. Such management of the land in addition to being less sensitive to fluctuations in the market value of crops, may have several important added benefits among which stand out retention of soil and of soil fertility and preservation of water resources (Gleissman *et al.*, 1981).

Apparently the major obstacle to a change of land management strategy would be economic. First, the crops, except for corn, are labour-intensive, and resources would be required to hire the extra human labour required. Second, some crops, such as cacao, coffee and allspice, required some technology (e.g. propane dryers to dry the seeds) to reach high productivity levels for processing before they can be marketed. Although only a few farmers at Los Tuxtlas have had enough resources to undertake the task of cultivating crops with a high market value and have diversified their private economics, such a situation suggests that a change in this direction rather than to continue with the horizontal expansion of cattle ranching could result in greater economic benefits to the local economics. Turning pasture land into agricultural parcels rather than turning more forest into pasture may thus result in reduction of biotic and physical isolation and in the persistence in time and space of forest wildlife. Unless a different model of land management is implemented in tropical regions such as Los Tuxtlas, cattle ranching will continue its horizontal expansion at the expense of the remaining forest. In this scenario, the ultimate fate of wildlife will be extinction and productivity of the local economies will continue to be insufficient to improve the quality of life of the people.

Clearly, we need long-term observations and basic ecological studies to assess the impact of land management practices on the survival of avian species. The limitation of our study is that it provides information only at one or two points in time on species presence in the landscape, but when taken as a diagnostic survey of how land management practices are affecting the conservation of species, we can derive some guidelines to ascertain the value of modifying such practices. Thus, our study suggests that in the landscape of Los Tuxtlas the presence of arboreal crops and even of non-arboreal crops may help, by acting as stepping stones, sustain bird populations and species present in the remaining forest fragments. A heterogeneous landscape matrix in which forest fragments, shaded and unshaded man-made habitats and live fences occur against a background of pastureland seemed to be a more benign arrangement of the land for segments of the remaining rain forest avifauna than pasture lands alone. In this scenario, the study of the dynamics of sources and sinks (*sensu* Pulliam, 1988) and their impact on the regulation of the populations of the remaining avifauna species, might be an adequate step to take to further improve the precision of conservation models at the landscape level.

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Appendix 1. Species detected at the various habitats studied. Values shown are the percentage of individuals contributed by each species to the total number of birds recorded per habitat

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Tinamidae													
Tinamus major	0.06											0.01	1800
Crypturellus boucardi	0.12											0.03	850
Ardeidae													
Bubulcus ibis			0.06		1.68	0.80	0.17				0.77	0.27	340
Cathartidae													
Coragyps atratus	0.08						0.09					0.03	1800
Cathartes aura		0.05										0.00	1400
Accipitridae													
Leptodon cayanensis	0.10											0.02	440
Elanus caeruleus								0.51				0.02	350
Rostrhamus sociabilis	0.02										0.77	0.03	380
Accipiter striatus						0.13						0.01	105
Accipiter cooperii									0.19			0.02	440
Leucopternis albicollis	0.39	0.20					0.09					0.12	725
Buteogallus anthracinus	0.12		0.18									0.04	800
Buteo nitidus	0.16	0.05	0.12		0.10							0.06	500
Buteo magnirostris	0.43	0.69	0.60	0.65	1.28	2.40	0.86	0.51	0.37		0.77	0.78	350
Buteo jamaicensis	0.02											0.00	900
Spizaetus tyrannus	0.02											0.00	1000
Spizaetus ornatus	0.02											0.00	1200
Falconidae													
Polyborus plancus	0.04											0.01	1000
Falco columbarius	0.04											0.01	160
Falco rufigularis	0.10											0.02	142
Falco peregrinus											0.77	0.02	610
Falco sparverius							0.09				1.54	0.06	115
Herpetotheres cachinnans	0.26	0.10			0.05	0.07	0.26				1.54	0.17	600
Micrastur ruficollis	0.02											0.00	175

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Micrastur semitorquatus	0.02											0.00	650
Cracidae													
Ortalis vetula	2.15	0.39	0.30				0.86					0.68	549
Penelope purpurascens	0.02											0.00	1700
Crax rubra	0.06											0.01	4000
Phasianidae													
Colinus virginianus					0.49							0.05	180
Columbidae													
Columba flavirostris	0.26	0.10	0.60		1.43	0.67	0.34					0.35	230
Columba nigirostris	0.79	0.20	0.12	0.16	0.20		0.69					0.35	162
Zenaida asiatica									0.93			0.09	145
Columbina inca	0.10				0.99	0.40		7.69			0.77	0.44	52
Columbina passerina							0.09	2.56	2.79			0.38	40
Columbina talpacoti	0.36	0.15	2.03	1.14	1.23	0.07	0.86	1.03	1.30			0.80	48
Claravis pretiosa		0.20		1.79								0.22	72
Leptotila rufaxilla	0.12	0.20		0.16		0.13						0.07	166
Leptotila verrauxi	0.04			0.32								0.05	165
Geotrygon montana	0.55	0.20										0.14	127
Psittacidae													
Aratinga nana	0.45	0.44			0.49							0.19	85
Amazona autumnalis	2.55	2.65	2.86	0.65	2.96	7.07	0.86					2.00	245
Cuculidae													
Coccyzus americanus	0.06				0.05	0.27						0.04	50
Piaya cayana	0.77	0.44	0.36	0.49	0.05		0.17					0.33	105
Crotophaga sulcirostris	0.83	0.39	0.18		5.57	0.67	8.94	15.38	1.86		2.31	3.09	82
Tytonidae													
Tyto alba					0.05							0.00	475
Strigidae													
Pulsatrix perspicillata	0.30											0.07	750
Glaucidium brasilianum	0.20	0.29	0.06	0.16	0.69		0.26					0.20	63

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Ciccaba virgata	0.43											0.09	300
Ciccaba nigrolineata	0.06											0.01	350
Lophostrix cristata	0.06											0.01	400
Caprimulgidae													
Nyctidromus albicollis	0.04		0.18				0.26					0.07	53
Nyctibiidae													
Nyctibius griseus	0.04											0.01	80
Trochilidae													
Phaethornis superciliosus	3.53	1.38	0.54	3.57	0.15	0.33	0.26					1.43	6
Phaethornis longuemareus	0.41	0.25		0.32						5.00		0.19	3
Camphylopterus excellens	0.28	0.10		0.97								0.18	8
Camphylopterus hemileucurus	0.97	0.93	0.83	2.60	0.20	0.20	0.26					0.73	11
Anthracothorax prevostii			0.24				0.17					0.05	4
Amazilia candida	1.42	1.92	1.85	1.95	1.82	0.27	0.86			10.00		1.25	4
Amazilia cynocephala	0.14	0.49	0.24		0.20	0.13						0.12	5
Amazilia tzacatl	0.06	0.49	0.06	1.14	0.20	0.40	0.26			15.00		0.39	4
Amazilia yucatanensis			0.12									0.01	5
Archilochus colubris					0.84		0.34					0.13	3
Trogonidae													
Trogon melanocephalus	0.28			0.16			0.17					0.11	68
Trogon violaceus	0.26	0.34	0.66	0.49	0.10		0.95					0.36	68
Trogon collaris	0.16						0.26					0.08	68
Trogon massena	0.02											0.00	145
Momotidae													
Hylomanes momotula	0.10											0.02	34
Momotus momota	1.30	0.39	0.77	0.97		0.33	0.26					0.56	140
Alcedinidae													
Chloroceryle americana	0.28	0.05				0.13						0.08	35
Chloroceryle aenea	0.02	0.05										0.01	16

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Ramphastidae													
Pteroglossus torquatus	1.01	2.31	1.37	2.92	0.25	0.27	1.20					1.11	198
Ramphastos sulfuratus	4.38	2.16	1.67	2.44	0.20	0.13	1.12					1.79	350
Picidae													
Melanerpes pucherani	0.24	0.74	0.66				0.09					0.19	60
Melanerpes aurifrons	4.24	7.86	8.76	4.22	10.30	6.54	4.73	1.54	2.60	10.00	0.77	5.38	65
Veniliornis fumigatus	0.12											0.03	45
Piculus rubiginosus	0.32											0.07	60
Celeus castaneus	0.16											0.04	60
Dryocopus lineatus	0.10	0.20			0.34	0.33	0.17		0.56			0.18	169
Furnariidae													
Automolus ochrolaemus	0.10	0.15										0.04	44
Xenops minutus	0.24	0.15										0.07	14
Dendrocolaptidae													
Dendrocincla anabatina	0.61	0.10										0.14	42
Sittasomus griseicapillus	0.59	0.69	0.30	0.49			0.09					0.29	13
Glyphorhynchus spirurus	0.16	0.05										0.04	19
Dendrocolaptes certhia	0.10											0.02	60
Xiphorhynchus flavigaster	1.30	0.29	0.30	0.65								0.41	48
Lepidocolaptes souleyetti	0.45	0.34	0.24	0.65	0.10		0.09					0.24	45
Formicariidae													
Thamnophilus doliatus	0.04						0.17					0.04	30
Tyrannidae													
Myiopagis viridicata	0.02											0.00	12
Elaenia flavogaster	0.02											0.00	
Attila spadiceus	0.55	0.25	0.18	0.16								0.18	46
Mionectes oleagineus	0.71	0.39	0.12	3.90			0.09					0.65	15
Leptopogon amaurocephalus	0.08	0.10	0.06									0.03	11
Rhynchocyclus brevirostris	0.20	0.10					0.09					0.07	20
Tolmomyias sulphurescens	0.04	0.34	0.06	0.16			0.17					0.09	15

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Platyrinchus cancrominus	0.99		0.06									0.23	10
Onychorhynchus coronatus	0.02											0.00	30
Myiobius sulphureipygius	0.20	0.15	0.06									0.06	15
Contopus borealis		0.15	0.36									0.04	32
Empidonax flaviventris	0.16	0.64		0.81	0.15		0.26					0.24	11
Empidonax traillii	0.06	0.10	0.60									0.07	11
Empidonax minimus	0.36	0.54	0.72		0.25	0.53	1.20					0.45	12
Empidonax sp.	0.10		0.42			0.07	0.26					0.10	12
Myiarchus tuberculifer	0.41				0.10	0.07						0.10	20
Myiarchus crinitus	0.04	0.20			0.10	0.20	0.09					0.06	34
Myiarchus tyrannulus	0.16	0.64	0.12	0.16	0.39	0.13	0.26					0.21	32
Pitangus sulphuratus	1.78	4.42	0.95	2.76	2.46	3.67	4.21	2.05	2.79	10.00		2.78	60
Megarynchus pitangua	0.51	0.93	1.19	0.32	0.64	1.20	0.86	0.51	0.19			0.65	62
Myiozetetes similis	0.71	1.13	1.31	0.65	0.69		0.86	2.56				0.73	45
Myiodynastes maculatus	0.08			0.32			0.09					0.07	50
Myiodynastes luteiventris	0.12	0.34	0.60	0.49	0.34	0.07						0.19	46
Tyrannus melancholicus	0.10	0.29	1.67		0.79		0.52	0.51				0.35	40
Tyrannus couchii	0.16	0.15	0.30	0.16			0.34					0.15	40
Tyrannus forficatus							0.26	2.05	2.42			0.35	45
Pachyramphus aglaiae	0.53	0.88	0.48	0.65	0.64	0.07	1.38					0.60	30
Tityra semifasciata	3.14	5.06	4.65	7.31	1.97	2.54	3.70					3.30	88
Tityra inquisitor	0.04	0.05	0.06	0.81	0.10							0.12	50
Cotingidae													
Cotinga amabilis	0.02											0.00	22
Pipridae													
Pipra mentalis	0.18	0.15		0.81								0.14	19
Corvidae	0.00												
Cyanocorax morio	4.97	11.98	10.31	1.62	9.07	18.15	4.73		0.74			6.10	285
Troglodytidae													
Campylorhynchus zonatus	2.41	7.71	1.91	2.44	3.35	1.13	3.52					2.64	30
Thryothorus maculipectus	1.12	0.15	0.72	1.46			0.17					0.51	14
Troglodytes aedon					0.05							0.00	15

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Henicorhina leucosticta	6.87	0.83	2.92	2.27			0.60					2.18	16
Muscicapidae													
Regulus calendula	0.04											1.01	13
Ramphocaenus melanurus	0.12											0.03	9
Polioptila caerulea	0.34	0.59			0.44	0.53	1.81					0.51	6
Polioptila plumbea	0.02						0.26					0.05	7
Myadestes unicolor	0.06	0.05		0.49								0.07	39
Catharus minimus	0.02											0.00	20
Catharus ustulatus	0.32	0.05		0.32	0.10	0.07						0.13	31
Hylocichla mustelina	1.48	0.69	0.18	2.27		0.07						0.66	47
Turdus grayi	2.09	1.67	0.48	3.73	0.05	2.74	0.77					1.39	72
Turdus assimilis		0.10		0.65								0.08	62
Mimidae													
Dumetella carolinensis	0.20	0.44		0.49		0.33	0.34					0.22	37
Vireonidae													
Vireo griseus	0.32	0.64	0.95	1.62	1.68	1.20	3.70	0.19				1.26	14
Vireo bellii	0.02		0.12		0.20							0.03	9
Vireo solitarius	0.06	0.05			0.05							0.02	17
Vireo flavifrons	0.08	0.10		0.16	0.10	0.13	0.43					0.14	20
Vireo gilvus						0.07	0.00					0.00	12
Vireo olivaceous	0.06	0.29	0.06									0.05	19
Hylophilus ochraceiceps	0.41	0.20										0.11	15
Hylophilus decurtatus	0.61		0.18				0.17					0.18	9
Emberizidae													
Vermivora pinus			0.06									0.00	9
Vermivora peregrina							0.17		0.37			0.07	8
Vermivora celata	0.02											0.00	8
Vermivora ruficapilla	0.04	0.15					0.17		0.56			0.11	9
Parula americana	0.06	0.29	0.77	0.16	2.12	0.60	0.69					0.47	8
Dendroica petechia	0.12		0.72	0.16	1.48	0.40	0.95		0.37			0.46	8
Dendroica pennsylvanica			0.06									0.00	9
Dendroica magnolia	0.67	1.62	1.67	2.27	4.19	6.14	4.04		0.93			2.25	13

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Dendroica caerulescens		0.10			0.10							0.02	9
Dendroica coronata	0.16	0.15	0.12		3.65		2.06		1.49			0.88	9
Dendroica virens	0.45	0.34	1.07	0.16	0.10	0.27	1.03					0.43	9
Dendroica fusca	0.02											0.00	10
Dendroica dominica					0.54							0.05	11
Dendroica palmarum						0.07			0.19			0.02	8
Mniotilta varia	0.67	0.49	0.42	0.65	1.03	2.47	0.77					0.69	18
Setophaga ruticilla	0.95	1.03	1.97	1.79	2.17	3.47	1.55		0.19			1.37	19
Helmitheros vermivorus	0.39		0.06									0.09	15
Seiurus aurocapillus	0.45	0.10		1.14		0.07						0.24	18
Seiurus noveboracensis	0.04			0.32		0.27						0.06	14
Seiurus motacilla	0.24	0.39		1.79		0.20						0.30	10
Oporornis formosus	1.07	0.29	0.30	1.46	0.05	0.13	0.09					0.48	10
Oporornis philadelphia		0.05	0.18									0.02	16
Oporornis tolmiei	0.04	0.05										0.01	16
Geothlypis trichas	0.04				0.20		0.43		0.56			0.15	12
Geothlypis poliocephala	0.02		0.24		0.10							0.03	7
Euthlypis lachrymosa	0.04											0.01	10
Wilsonia citrina	1.62	1.92	2.15	1.62	1.92	2.94	1.29					1.47	12
Wilsonia pusilla	0.83	1.57	3.52	1.30	1.13	1.33	2.67		0.74			1.45	25
Myioborus miniatus	0.02											0.00	10
Basileuterus culicivorus	1.66		0.12				0.17					0.41	11
Basileuterus rufifrons	0.26	0.10	0.77	0.16			1.38					0.38	18
Basileuterus belli	0.02											0.00	12
Icteria virens	0.12	0.34			0.64	0.20	0.09		0.19			0.16	15
Coereba flav eola				0.65		0.20						0.09	12
Cyanerpes cyaneus	0.04			0.65								0.08	38
Euphonia affinis	0.04	0.00										0.01	36
Euphonia hirundinacea	1.28	0.74	1.07	0.65	0.05	0.33	1.03					0.71	27
Euphonia gouldi	0.04						0.17					0.04	35
Thraupis episcopus	0.20				0.20		0.09					0.08	35
Thraupis abbas	1.18	0.34	0.89	2.92	1.68	0.27	0.86					1.00	40
Eucometis penicillata	0.04	0.10										0.02	40

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Lanio aurantius	0.61	0.10		1.30								0.29	15
Habia rubica	1.28	0.05	0.18	0.49								0.36	44
Habia fuscicauda	7.85	0.83	0.60	2.92	0.05		2.06					2.55	16
Piranga rubra	0.73	0.64	0.42	0.65	0.49	1.60	1.12					0.67	81
Piranga leucoptera		0.88										0.08	50
Ramphocelus sanguinolenta				0.32								0.04	40
Ramphocelus passerinii		0.10	0.12									0.02	31
Chlorospingus ophthalmicus	0.04			0.16								0.03	45
Saltator maximus	0.04	0.54		0.32								0.09	35
Saltator atriceps	1.32	0.98	0.06	1.14			1.98					0.85	47
Caryothraustes poliogaster	0.02			0.16			0.17					0.05	18
Pheucticus ludovicianus		0.05	0.12									0.01	15
Pheucticus melanocephalus			0.54									0.04	25
Cyanocompsa cyanoides	0.10	0.05		0.32	0.05							0.07	10
Cyanocompsa parellina	0.04		0.24									0.03	10
Guiraca caerulea		2.41							0.93			0.31	31
Passerina cyanea	0.24	0.29	0.36			0.80		1.54	3.35			0.54	14
Passerina versicolor							0.09					0.01	11
Passerina ciris							0.26					0.04	15
Spiza americana								10.26				0.36	28
Arremonops rufivirgatus	0.02		0.42									0.04	25
Volatinia jacarina	0.02	0.15					0.43		3.16			0.40	10
Sporophila aurita									0.37			0.04	12
Sporophila torqueola	0.08		1.49	0.16	0.15		0.17	4.62	4.46	15.00	0.77	0.92	10
Tiaris olivacea		0.05	0.12					2.56	0.19	5.00		0.16	10
Aimophila rufescens			0.12									0.01	36
Chondestes grammacus								3.59				0.13	25
Melospiza lincolnii								2.05				0.07	16
Sturnella magna	0.02				0.10		1.63	6.67			26.17	1.34	85

Appendix 1. (*Continued*)

Species	Forest	Cacao	Coffee	Mixed	Citrus	Allspice	Live fence	Jalapeño	Corn	Banana	Pasture	Total	Average mass (g)
Dives dives	1.66	7.12	6.97	0.49	13.26	17.21	9.11	21.03	43.31	25.00	63.11	12.62	100
Quiscalus mexicanus	0.20	0.93	10.49		5.82	1.53	2.58	10.77	21.75	5.00		4.52	150
Molothrus aenus			0.83									0.06	68
Icterus dominicensis	0.12	0.25										0.05	32
Icterus spurius					0.39							0.04	20
Icterus cucullatus	0.08	0.05		0.16	0.20							0.06	45
Icterus mesomelas		0.20										0.02	70
Icterus gularis		0.39			1.03	0.13	1.12					0.33	75
Icterus graduacauda		0.29		0.32			0.17					0.09	43
Icterus galbula	0.12	0.05		0.81	0.69		0.43					0.26	34
Amblycercus holosericeus	0.10	0.10	0.06									0.04	65
Psarocolius wagleri	0.43	1.08	0.24	1.30	0.20							0.37	175
Psarocolius montezuma	3.16	1.57	2.15	4.87	0.54	4.67	1.55					2.18	380
Fringillidae													
Carduelis psaltria												0.03	10
Species	178	123	98	86	82	65	97	21	31	9	12	226	
Individuals	4932	2036	1678	2464	2029	1499	3722	780	2152	160	693	22145	