Songbird Use of Gallery Woodlands in Recently Cleared and Older Settled Landscapes of the Selva Lacandona, Chiapas, Mexico

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Abstract: *Many regions of Central America have undergone wide-scale habitat change as land has been converted for cultivation or grazing. Clearing for agriculture often leaves a variety of regenerating and remnant patches of wooded vegetation. Of particular importance is arroyo vegetation, or strips of trees or tall shrubs growing along streams. Although it is widely acknowledged that tropical arroyo vegetation supports high densities of birds, as avian habitat it remains poorly studied. We used point counts to study populations of migrant and resident songbirds in the arroyo vegetation of settled areas of the Selva Lacandona adjacent to the Montes Azules Biosphere Reserve of southeastern México. Two study areas were established on lands that had been cleared and settled 20–35 and 10 years previously. Our objectives were to assess the value of arroyo vegetation to the conservation of avian species diversity and abundance in agricultural landscapes and to compare the composition and abundance of songbirds in cleared areas settled at different times over a 35-year period. Arroyo vegetation had a wide diversity of songbird species that, in overall terms, differed little between those landscapes cleared recently and those cleared up to 35 years previously. In both areas we found a high abundance of habitat generalists and a smaller number of forest-dependent species, particularly migrants. Loss of forest specialists occurs rapidly, with little further loss as the arroyos become increasingly isolated. Our data also suggest that birds do not crowd into limited habitat as the surrounding vegetation is eliminated, implying that the overall carrying capacity of the agricultural landscape is greatly enhanced as larger areas of arroyo vegetation are protected. Protection of arroyo vegetation will increase the diversity of birds living in agricultural areas and can be achieved simply by expanding upon land-use practices currently in use.*

Uso de galerías boscosas por aves cantoras en paisajes recientemente clareados y en paisajes poblados con anterioridad de la Selva Lacandona en Chiapas, México

Resumen: *Muchas regiones de Meso-América han pasado por cambios a gran escala en sus habitats, debido a que las tierras han sido transformadas para el cultivo o pastoreo. Los clareos para la agricultura dejan a menudo una variedad de parches de vegetación leñosa en regeneración y remanentes. De particular importancia resulta la vegetación de los arroyos, o fajas de árboles o arbustos altos que crecen a lo largo de los arroyos. Si bién es ampliamente reconocido que la vegetación de arroyos tropicales mantienen altas densidades de pájaros, la misma sigue siendo poco estudiada como hábitat para aves. Utilizamos conteos puntuales para estudiar poblaciones de aves cantoras residentes y migratorias, en la vegetación de los arroyos de áreas pobladas de la Selva Lacandona adyacentes a la Reserva de la Biósfera de los Montes Azules en el sureste de México. Se establecieron dos áreas de estudio en tierras que han sido clarladas y pobladas hace 20-35 y 10 años. Nuestros objetivos eran evaluar el valor de la vegetación de los arroyos para la conservación de la diversidad específica y la abundancia de las aves en paisajes agrícolas y comparar la composición y abundancia de las aves cantoras en áreas clareadas que fueron pobladas en distintos momentos a lo largo de un peri-*

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odo de 35 años. La vegetación de los arroyos tuvo una ámplia diversidad de especies de aves cantoras que en términos generales, diferian poco entre los paisajes clareados recientemente y aquellos clareados hasta 35 años antes. En ambas áreas encontramos una alta abundancia de generalistas del hábitat y un menor número de especies dependientes de los bosques, particularmente especies migratorias. La pérdida de los especialistas de los bosques ocurre rápidamente y es seguida de una pérdida menor a medida que los arroyos se hacen más aislados. Nuestros datos sugieren también que las aves no se apiñan dentro de un hábitat limitado a medida que la vegetación que la rodea es eliminada, lo que implica que la capacidad de carga total del paisaje agrícola aumenta considerablemente con la protección de áreas más grandes de vegetación de los arroyos. La protección de la vegetación de los arroyos incrementará la diversidad de aves que viven en áreas agrícolas y puede ser alcanzada simplemente mediante la extensión de las prácticas de uso de la tierra actualmente en uso.

Introduction

Wide-scale conversion of Neotropical forests to cropland, pasture, or second-growth scrub has greatly altered the amount and quality of habitat availaible to forest birds in Middle America since 1950. Estimates of deforestation rates for the decade ending in 1990 show the long-term mean rate of conversion to be holding steady at just under 2% per year for Mexico and Central America (World Resources Institute 1992). Studies focusing on Mexico estimate current rates of wet tropical forest loss to be slightly higher, ranging from 3% to 4% (R. Dirzo personal communication). Whatever the precise rate of deforestation, loss of forest across this region has been extensive, leaving just over 28% in native forest cover (World Resources Institute 1992).

Despite these dramatic changes to the vegetative cover of Middle America, the transition from large expanses of forest to an agricultural or pastoral landscape has seldom been complete (Whitmore & Sayer 1992). Remnants of forest frequently are left in place during clearing, and patches of second growth regenerate in remote and less accessible locations. In addition, when land is cleared for cattle grazing or cultivation, bands of vegetation often are left along streams, or trees and shrubs are allowed to regrow at these sites (arroyo vegetation). As a result, current land-use practices have left a mosaic of cleared, regenerating, and unaltered patches of tropical vegetation across the region.

Dotting the agricultural landscape of Middle America as they do, patches of arroyo vegetation may represent an important refuge for a wide variety of taxa, but their conservation value to landbirds has been studied little. Perhaps this is because fragmentation has negative implications for conservation of ecosystems. Within the context of an agricultural landscape, however, small patches may provide habitat for some of the original forest species and certainly support generalist species that still require some type of wooded vegetation. Furthermore, the sheer extent of pasture and fields in Middle America means that small changes in habitat management adopted across local levels may have a large regional impact.

The limited ornithological research conducted in tropical forest patches indicates that migratory landbirds may commonly use such habitat across the region during the nonbreeding season (Hutto 1980; Greenberg 1992; Robbins et al. 1992; Villaseñor 1993; Salgado Ortiz 1993). One key question is how bird populations fare in forest remnants over the long run. There are two issues related to temporal stability: (1) the stability of the wooded fragments themselves and (2) the integrity of bird populations as the landscape is increasingly cleared and isolated from continuous forest. The size and distribution of forested patches are often dynamic, shrinking (Powell et al. 1992) or expanding (Janzen 1988) depending upon the social structure and land management practices of the local people (Browder 1993).

Our study was conducted in and around the Montes Azules Biosphere Reserve. The Lacandon Forest, of which this reserve is a part, has been colonized by waves of immigrants over the past 40 years. We examined the long-term stability of bird use of arroyo vegetation by taking advantage of the known history of settlement. We present one of the first systematic surveys of arroyo vegetation in a tropical agricultural landscape, and we examine the probable changes that occur with increased age of settlement by comparing recently cleared areas and those of areas settled over a 35-year period. Because of their abundance in arroyo vegetation of the region, we focused on the response of migratory songbirds.

Methods

Study Area

The Selva Lacandona, contained in part within the Montes Azules Biosphere Reserve, lies in the northeastern corner of Chiapas, Mexico, near the Guatemalan border (Fig. 1). The landscape of the study area is characterized

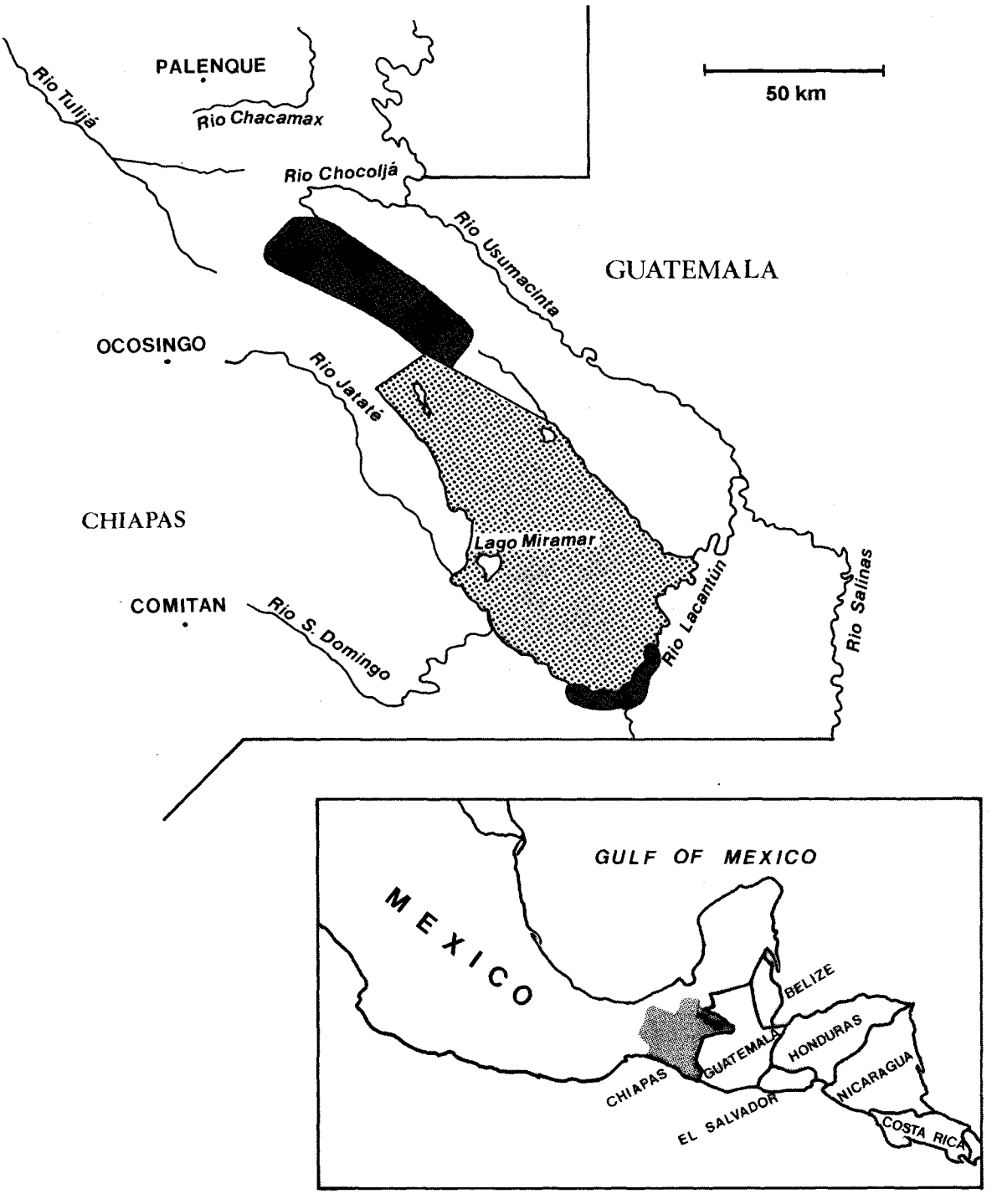

Figure 1. Map of northeastern Chiapis, Mexico, showing the boundaries of the Montes Azules Biosphere Reserve (lightly shaded) and the two study areas (darkly shaded), Chajul in the south and Damasco in the north.

by a series of parallel northwest-southeast ridges reaching elevations of 200 to 1000 meters, with valley floors as low as 100 meters in the eastern portion of the region. The mature vegetation cover for the lower elevation areas is medium-tall, wet tropical forest. The climate is typically hot and humid, with temperatures ranging from 14°C to 38°C throughout the year and a mean annual temperature of 25°C (Garcia 1988). Rainfall across the region varies from 1700 to 3300 mm (mean = 2500 mm), with dry periods occurring in the months of Feb-

ruary through June and either July or August (Garcia 1988).

Calleros and Brauer (1983) report data from 1875 that indicate that the Selva Lacandona originally covered 1.25 million ha. The Lacandon people, for whom the forest is named, lived in small, isolated communities across the region until colonization by outsiders started in the mid-1950s (De Vos 1988). In 1954, logging companies began work in the most accessible areas at the north end of the forest. At the same time, colonizers from other parts of Mexico began to enter the region, using slash-and-burn technology to clear land for planting subsistence crops. From 1964 to 1975, the rate of deforestation increased as logging companies introduced mechanized logging to the country; this brought the estimated total area of forest lost to nearly 400,000 ha (about 32% of the total original area; Calleros & Brauer 1983). To protect the central core of the Selva Lacandona, in 1978 the Mexican government created the Montes Azules Biosphere Reserve covering 331,200 ha (De Vos 1988). By 1982, deforestation had affected 42% of the original forest area (Calleros & Brauer 1983) and although more recent estimates have not been published, clearing has continued up to the present time, converting more of the selva to agricultural uses, primarily cattle pasture.

Due to changing political necessity and differences in physical accessibility, zones around the reserve have been settled at different times (De Vos 1988). Colonization of the northern portion began in the mid-1950s; further encroachment in the north and opening up of the eastern and western regions occurred from 1960 through 1964. A flood of refugees from Guatemala in 1981 and the construction of a road along the Guatemalan border by the Mexican government resulted in the colonization of the regions south and southeast of the reserve. The cultivated land in this region is now primarily used for cattle ranching. In more recently colonized parts of the study area, forest remnants are in less accessible or infrequently used locations such as hill tops and steep slopes. These patches tend to be less isolated from other vegetation, surrounded by more second growth, and more extensively linked to other forest remnants through riparian corridors than patches in areas that have been settled for longer periods. Older areas tend to be more extensively managed for cattle, leaving fewer patches of wooded vegetation, which are primarily located along streams.

Habitats Sampled

We conducted point counts during the winters of 1991-1992 and 1992-1993 in woody vegetation associated with the rivers and streams in the valleys of the study area. We refer to habitats along streams in aggregate as arroyo vegetation. This arroyo vegetation is typically 5-25 meters wide in the region where we were sampling, although some may be considerably wider. This pattern of land use creates at least four distinguishable types of riparian habitat: (1) scrub, in which the vegetation consists of often dense herbaceous and woody vegetation generally less than 6 meters tall; (2) gallery forest, where tall, woody vegetation creates a distinct overstory above 8 meters bordering the stream with a woody and/or herbaceous understory; (3) shade woods, similar to gallery forest with tall, woody vegetation creating a distinct overstory at least 8 meters tall but lacking any understory vegetation; and (4) remnant forest, tall, woody vegetation with remnants of original forest. Although the first two categories were relatively common, the latter two were encountered less frequently, particularly in areas that had been under cultivation for longer periods.

Two areas in the vicinity of the reserve were sampled for this study. During the winter of 1991-1992, data were collected in the Marquez de Comillas, immediately across the Río Lancantún from the southern end of the Montes Azules Biosphere Reserve (Fig. 1); this is referred to as the Chajul study area. The area was one of the most recently colonized in the Selva Lancandona, the *ejidos* (community controlled lands) having been established since 1979-1981. Clearing had primarily occurred 10 years prior to our study but continued at much lower rates up to the time of our study. Most of the clearing has been within 1-2 km of the river, and the arroyo vegetation we sampled averaged 507 meters (60-1200 m) from high graded forest on the Marquez de Comillas side. Sampling in the winter of 1992-1993 covered a broader area on the northeast side of the reserve (Fig. 1), which is referred to as the Damasco study area. Settlements in this region vary in age from 20 to 35 years, and forest cover was usually more than 6 km from specific study sites (range 0.5-15 km). The total number of point counts conducted in the Chajul area was necessarily smaller than in the Damasco region because the total area cleared for pasture in the *ejidos* around Chajul was substantially smaller.

Habitat Analyses

Habitat availability on a broad scale of the two study areas was examined through the use of remote sensing. Data from Landsat TM images were acquired for the Damasco area from January 1989 and February 1990. Information from bands 3, 4, and 5 were downloaded to computers at the Maine Image Analysis Laboratory, University of Maine, to be analyzed using ERDAS and ARC/INFO software. Data were analyzed using the unsupervised classification approach to identify the 20 most common spectral signatures. A preliminary habitat map was produced by assigning each of the 20 spectral classes to the apparent habitat type. Assignments were made based on the comparison of classified and unclassi-

fied imagery as well as analysis of spectral separability indices for the signatures. Four broad-scale habitat types were identified: (1) medium-tall broadleaf forest (old growth), (2) low broadleaf forest (tall second growth), (3) broadleaf forest scrub, and (4) herb-dominated clearing (pasture). Ground-truthing information and 1:50,000 topographic maps were used in post-classification editing, and the imagery was smoothed using a 3-by-3 pixel filter with a 1-pixel threshold. This resulted in the classification image having a minimum mapping unit of about 0.56 ha. Perennial and intermittent streams were digitized onto the image from the 1:50,000 topographic maps, and stream buffers of 50 meters and 100 meters were delimited to examine the amount of habitat available in arroyos.

Remote-sensing data from the Chajul area were acquired for January 1989 in the form of a photographic print (1:100,000 scale) of one Landsat TM quarter scene. Analysis included the area within 5 km on either side of the Río Lacantún, from Ixcan to Reforma Agraria. Habitats were classified into the four broad categories outlined above, and spatial analyses were conducted using a digitizing program (Sigma-Scan; Jandel Scientific, Corte Madera, CA 94925) to determine total areas covered by each habitat.

Point Counts

Point count analyses were based on a subsample of the total data set. As such, they incorporate only data collected from the dry season (late January through March). We included all individuals encountered on a single visit to each survey point, except those flying over the count circle. Observers walked along an arroyo, stopping every 150–200 meters to conduct a count. Counts were conducted for 10-minute periods and included all individuals detected by sight or sound and known to be perched within a 25-meter radius of the point-count center. Sampling was conducted between 0630 hours and 1030 hours. Because of the linear nature of the habitat sampled, points were frequently at or near habitat boundaries. Within an arroyo system, we collected up to 20 points, but all points were at least 150 meters straight-line distance from all other sampled locations.

During the winter of 1991–1992, some sampling in the Chajul region was accompanied by the playing of a tape of Yellow-bellied Flycatcher (*Empidonax flaviventris*) calls and song as part of an associated study. A three-minute tape of two calls and one song was played at the beginning of each sampling period, followed by seven minutes without the tape. But the correlation between the number of individuals per migratory species encountered during survey periods using this tape and the number encountered when not using the tape was high ($r = 0.78$). More important, the regression line (number of birds detected per species with tape = 0.18 + 0.95 [birds/species detected without tape]) had a Y intercept near zero and a slope close to 1.0, suggesting no influence of the taped calls and song on numbers of migrants detected. We therefore used these untransformed data to compare with surveys conducted in 1992–1993 without the tape.

We used an independent data set (Salgado Ortiz 1993) to classify the broader habitat affiliations of the species observed in arroyo point counts and to compare habitat used by the same species at the two study sites. These were obtained from six transects run through intact broadleaf forest, habitat characterized by forest patches, and pasture habitat. The successional scope of the data allowed us to develop a broader picture of the habitat distribution of species found in arroyo vegetation. One-km transects in each habitat type were sampled in the winter of 1991-1992. Transects were 40 meters wide, 20 meters on each side, and flagged every 50 meters. Researchers slowly walked along the transect at a rate of approximately 400–500 meters per hour and recorded bird sightings by transect unit. Each transect was censused weekly through the winter, with the starting point alternated from end to end. Relative rates of detection in each of the three habitat types were calculated for each species with 20 or more individuals recorded. Niche breadth then was estimated using Levin's (1968) measure ($1/\Sigma p_i^2$). With three habitat types included, the maximum possible habitat breadth was 3.0, representing a species equally distributed within the habitat available. When species were strongly specialized in the type of habitat occupied, the narrowest possible index was 1.0, with all or the majority of individuals found in a single habitat type. In our classification scheme, those species with index values approaching the former (2.31 to 3.0) were termed broad generalists; those with values approaching the latter (1.0 to 1.30) were termed strong specialists. Species with intermediate values between 1.30 and 2.31 were moderate specialists, with the names of the two most commonly frequented habitats used to differentiate specializations. Based on this index of habitat breadth, species were categorized as broad generalists or as moderately specialized in or strongly affiliated with either broadleaf forest, pasture habitat, or forest patches.

To test for possible differences in the initial species composition of the two study areas prior to deforestation, we examined point-count data from intact forest habitat in the two areas. Data for the Chajul area were collected in the winter of 1991–1992; those for Bonampak (the continuous old-growth forest nearest to the Damasco area) were collected January through March 1991 and 1992. The abundance of all migrant and resident species encountered on point counts conducted in representative tropical rain forest of the two main study areas was compared through calculation of a Pearson correlation coefficient.

Table 1. Habitat availability in the two study areas in the Selva Lacandona presented as hectares and percent composition.

Habitat Type	*Damasco*	*Chajul*
Medium-Tall Broadleaf Forest	14,000 (19.1)	18,000 (79.6)
Low Broadleaf Forest	12,600 (17.2)	1900 (8.4)
Broadleaf Scrub	34,500 (47.1)	1700 (7.5)
Herb-Dominated Clearing	12,100 (16.6)	1000 (4.5)

Statistical Analysis

All data were tested for normality and homogeneity of variance; statistically significant differences were accepted at the 0.05 level. Because of the unequal distribution of sampling (both in terms of number of point counts and number of individuals detected) across habitat types and between study areas, any differences in species richness observed may have been an artifact of variable sample size (James & Rathbun 1981). To compare total species richness across the sampled habitats, we standardized our samples on the basis of the number of individuals detected. Based on this rarefaction procedure (using a program modified for C-language from Simberloff 1978), we examined the number of species accumulated after the detection of 160 individuals.

Results

Comparison of Forest Cover and Avifauna

Old-growth forests of the Chajul region were still relatively intact in 1989, nearly 10 years after settlement began in the early 1980s. Fully forested habitat was common, and medium-tall broadleaf forests covered 80% of the area sampled (Table 1). North of the Río Lacantún, within the official boundaries of the biosphere reserve, little or no development had occurred. South of the river large patches of converted land existed, but extensive tracts of forest, often high-graded for large trees, were still in place. The vegetation adjacent to most arroyos had not been removed or had been left to regrow.

Over 80% of the valley floors in the Damasco study area were in some vegatative cover other than the representative forest type, medium-tall broadleaf forest (Table 1). More-extensive forest remnants existed along the ridge tops between valleys, but on the valley floor remnants were typically small and scattered, covering an average of 10–20 ha. Large stretches (60%) of gallery woods in this area had been cleared of all vegetation.

Comparison of species abundance in continuous forest between Chajul and Bonampak (nearest forest to Damasco area) revealed a high correlation (Pearson's correlation coefficient $r = 0.91$, Fig. 2). This indicates that the arroyo study sites adjacent to these forest areas were also very similar in their avifaunal composition prior to deforestation and that further analyses comparing the post-clearing avifauna are warranted on this basis.

Diversity and Density of Birds

Data from 370 points are included in these analyses (Table 2). Within habitat types, migrants constituted from 20% to 31% of species detected. There was a significant positive correlation between effort (reflected in the number of point counts made in a habitat type) and the number of species detected. The greater the effort, the more resident species seen ($r_s = 0.89$, $n = 6$, $p < 0.05$); the same relationship did not hold true for migrant species ($r_s = 0.81$, $n = 6$, NS). Due to the consequential accumulation of resident species across study areas, migrants made up just over 18% of all species for both Damasco (31 of 166 species) and Chajul (26 of 141 species). Migrants made up 42% of all individuals (1364 of 3282) in Damasco and 39% (390 of 988 individuals) in Chajul. Neither the differences in species nor the differences in number of individuals between the two study areas were statistically significant (χ^2).

The mean number of resident individuals detected per point did not vary significantly across the six habitats for either study area ($F_{5364} = 1.71$, $p = 0.1318$). With the exception of shade woods, which had significantly

Table 2. Descriptive statistics for point counts conducted in Damasco and Chajul, Chiapas.

Statistic	*Damasco Gallery*	*Scrub*	*Chajul Gallery*	*Forest*	*Shade*	*Scrub*
Number Point Counts	187	84	26	19	23	31
Number Individuals Seen	2332	950	309	167	194	318
Number Migrant Species	31	26	20	19	18	19
Number Resident Species	125	86	55	44	41	52
Migrants as % of All Species	19.8	23.2	26.7	30.1	30.5	26.7
Migrants as % of All Individuals	41.8	40.9	35.2	44.9	40.2	40.3
Mean (SD) Individual per Point						
Migrants	5.2 (3.0)	4.6 (2.9)	4.2 (3.2)	3.9 (3.1)	3.4 (1.9)	4.1 (2.3)
Residents	7.3 (5.3)	6.7 (4.1)	7.7 (6.4)	4.8 (2.8)	5.0 (4.6)	6.2 (5.6)
Rarefaction ($n = 160$)						
Estimated Species (SD)	65.4 (3.9)	57.4 (3.6)	59.4 (2.7)	61.9 (0.9)	53.4 (1.9)	54.8 (2.7)

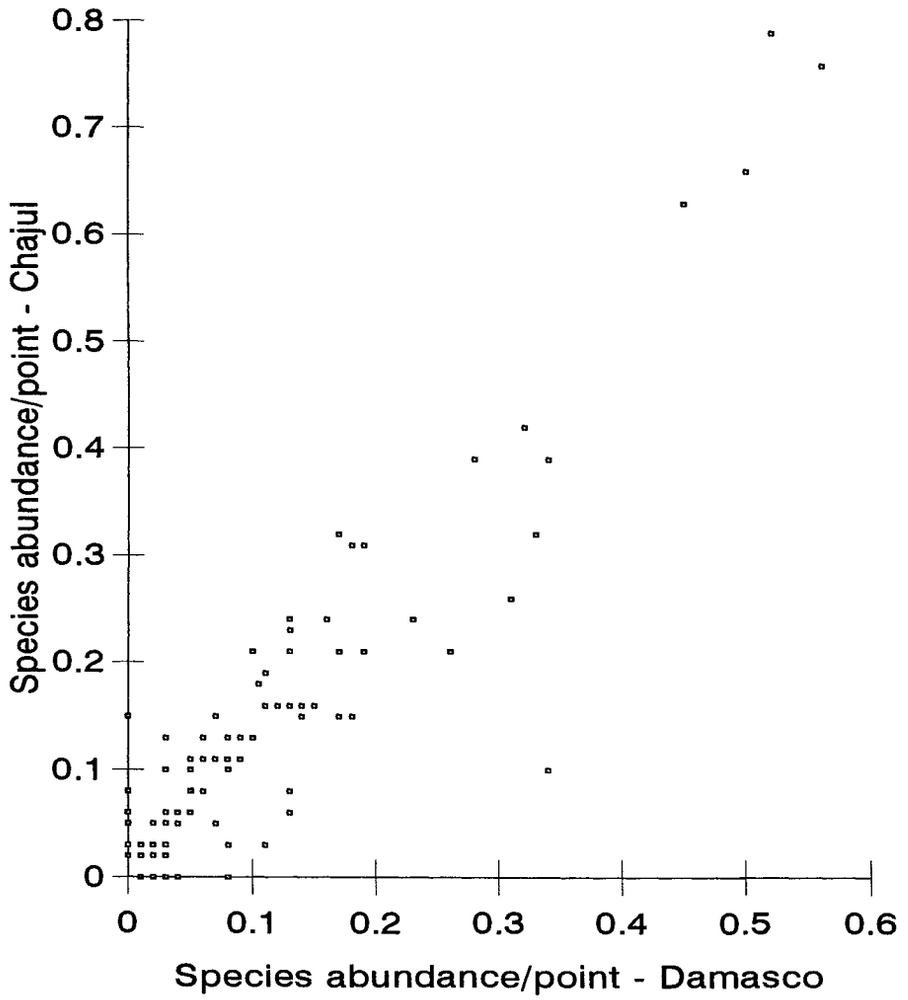

Figure 2. Comparison of species abundance (number of individuals per species per point count) for migrant and resident species at tropical forest sites in the Chajul and Damasco study areas.

fewer migrants per count than did Damasco gallery forest, the mean number of migrant individuals detected per point count showed little variation between habitats ($F_{5364} = 2.70, p = 0.0206$; SAS, Proc GLM; SAS Institute 1989). Within the same habitat type in the two study areas there were significant differences in the mean number of individuals encountered for a number of species (Table 3). This resulted in substantial changes in the rank order of species between similar habitat types in the two study areas.

Using rarefaction analyses, we found that the level of species richness in shade woods was different from that of both remnant forests (separation of 95% confidence intervals occurring at 130 individuals, Fig. 3a) and Damasco gallery forest (separation occurring at 160 individuals, Fig. 3b). No other pair-wise comparisons revealed significant differences between habitats in the number of species accumulated. Also, there were no significant differences in the number of migrant species accumulated after 70 individuals for any of the six habitats when they were tested by rarefaction.

Habitat Affiliation of Birds

Allocation of the top 40 species seen in each habitat to one of three habitat breadth types revealed some differences in the species found in the two study areas sampled (Table 4). There was a higher concentration of forest-specialist species than open-field species among the Chajul data than for the Damasco data set (Table 4). This is particularly true for the top 20 species and for migrants as a group; the pattern was less clear among the subsequent 20 species and resident species.

Forest-specialist migrant species persisted in small numbers in the arroyo vegetation of both the Chajul and Damasco regions. Only the Yellow-bellied Flycatcher was found in substantial numbers, however, and then primarily in the Chajul region. Other forest specialists, such as the Kentucky Warbler (*Oporornis formosus*) and Hooded Warbler (*Wilsonia citrina*), were encountered at low densities in both areas (see Table 3 for those species ranked among the top 10). Wood Thrush (*Hylocichla mustelina*) was extremely scarce in arroyo

Table 3. Comparison of abundances for the top 10 species found in gallery forest and scrub habitat of Chajul and Damasco.*

	Chajul			*Damasco*			
Species	*Rank*	*Mean*	*SE*	*Rank*	*Mean*	*SE*	*t-test* p *Value*
Gallery Forest Migrants							
Wilson's Warbler							
Wilsonia pusilla	1	0.61	0.11	4	0.37	0.04	0.033
Yellow Warbler							
Dendroica petechia	2	0.53	0.11	8	0.29	0.04	0.031
Yellow-bellied Flycatcher							
Empidonax flaviventris	3.5	0.46	0.11	18	0.07	0.02	0.002
Northern Oriole							
Icterus galbula	3.5	0.46	0.32	6.5	0.32	0.07	0.675
American Redstart							
Setophaga ruticilla	5	0.35	0.10	1	0.79	0.05	0.0002
Orchard Oriole							
Icterus spurius	6	0.31	0.21	18	0.07	0.02	0.261
Tennessee Warbler							
Vermivora peregrina	7	0.23	0.19	28	0.01	0.01	0.257
Magnolia Warbler							
Dendroica magnolia	8	0.15	0.07	2	0.75	0.05	0.0001
Northern Waterthrush							
Seiurus noveboracensis	11	0.12	0.06	6.5	0.32	0.04	0.008
Summer Tanager							
Piranga rubra	11	0.12	0.06	14	0.12	0.02	0.974
Common Yellowthroat							
Geothlypis trichas	11	0.12	0.06	9	0.21	0.03	0.200
Least Flycatcher							
Empidonax minimus	11	0.12	0.06	5	0.36	0.04	0.002
Yellow-breasted Chat							
Icteria virens	11	0.12	0.08	10	0.19	0.03	0.420
Gray Catbird							
Dumetella carolinensis	0			3	0.41	0.07	
Scrub Migrants							
Yellow Warbler	1	0.61	0.10	6	0.31	0.05	0.005
Least Flycatcher	2.5	0.55	0.09	3	0.49	0.07	0.62
Gray Catbird	2.5	0.55	0.15	4	0.46	0.08	0.60
Wilson's Warbler	4	0.42	0.11	8	0.23	0.05	0.08
Orchard Oriole	5	0.39	0.22	14	0.08	0.03	0.17
Magnolia Warbler	6	0.26	0.08	1	0.75	0.08	0.0001
Indigo Bunting	7.5	0.23	0.09	10.5	0.17	0.06	0.59
Passerina cyanea							
Yellow-breasted Chat	7.5	0.23	0.08	9	0.21	0.05	0.90
Summer Tanager	9.5	0.16	0.07	13	0.12	0.06	0.58
Yellow-bellied Flycatcher	9.5	0.16	0.07	20.5	0.02	0.02	0.055
American Redstart	11.5	0.13	0.06	2	0.57	0.07	0.0001
Common Yellowthroat	11.5	0.13	0.06	5	0.33	0.06	0.021
Northern Waterthrush	17	0.03	0.03	7	0.25	0.05	0.0004
Gallery Forest Residents							
Melodious Blackbird							
Dives dives	1	0.65	0.19	6	0.27	0.05	0.063
Social Flycatcher							
Myiozetetes similis	2	0.50	0.19	4	0.36	0.06	0.430
Yellow-throated Euphonia							
Euphonia hirundinacea	3	0.46	0.39	5	0.28	0.06	0.650
Buff-throated Saltator							
Saltator maximus	4	0.42	0.17	18.5	0.12	0.04	0.102
Band-backed Wren							
Campylorhynchus zonatus	6	0.34	0.25		0.04	0.03	0.240
Blue-gray Tanager							
Thraupis episopus	6	0.34	0.17	7	0.26	0.05	0.590
Rufous-tailed Hummingbird							
Amazilia tzacatl	6	0.34	0.11	1	0.50	0.05	0.290
Clay-colored Robin							
Turdus grayi	8	0.31	0.11		0.05	0.03	0.007

Table 3. Continued

Species	Chajul			Damasco			t-test p Value
	Rank	Mean	SE	Rank	Mean	SE	
Golden-masked Tanager *Tangara larvata*	9	0.27	0.15		0.04	0.02	0.144
Spot-breasted Wren *Thryothorus maculipectus*	10	0.23	0.10	2	0.42	0.06	0.106
White-collared Seedeater *Sporophila torqueola*		0.04	0.04	3	0.38	0.10	0.001
Blue-gray Gnatcatcher *Polioptila caerulea*		0		8.5	0.22	0.03	
Red-throated Ant-Tanager *Habia fuscicauda*		0		8.5	0.22	0.05	
Little Hermit *Phaethornis longuemareus*		0.12	0.06	10	0.15	0.03	0.666
Scrub Residents							
Scarlet-rumped Tanager *Ramphocelus passerinii*	1	0.68	0.21	19	0.10	0.04	0.012
White-collared Seedeater	2	0.48	0.28	2	0.49	0.11	0.98
Rufous-tailed Hummingbird	3	0.39	0.08	1	0.73	0.09	0.007
Blue-black Grassquit *Volatinia jacarina*	4	0.35	0.15	7.5	0.24	0.10	0.53
Spot-breasted Wren	5	0.29	0.12	5	0.32	0.06	0.80
Crimson-collared Tanager *Phlogothraupis sanguinolenta*	6	0.26	0.26		0.02	0.02	0.37
Yellow-billed Cacique *Amblycerus holosericeus*	7	0.19	0.10		0.02	0.02	0.09
Groove-billed Ani *Crotophaga sulcirostris*	8	0.19	0.19		0		
Yellow-throated Euphonia	9	0.16	0.09	9.5	0.23	0.08	0.60
Black-headed Saltator *Saltator atriceps*	10	0.13	0.08		0.07	0.04	0.48
Social Flycatcher		0.06	0.06	3	0.39	0.08	0.002
Blue-gray Tanager		0.03	0.03	4	0.36	0.13	0.015
Melodious Blackbird		0.06	0.06	6	0.27	0.07	0.033
White-tipped Dove *Leptotila verreauxi*		0		7.5	0.24	0.05	
Blue-gray Gnatchatcher		0.03	0.03	9.5	0.23	0.06	0.008

**Comparison was based on t-test for which p-values are reported in the last column. Abundance is defined as mean number of individuals encountered per point.*

vegetation and was the only forest-migrant species not detected in the Damasco region.

Resident forest specialists were generally rare both in the arroyo vegetation of the recently cleared Chajul region and in the more settled Damasco region. Small numbers of forest specialists were found in both areas, but none of them were among the most common resident species. Green Jay (*Cyanocorax yncas*; mean number seen per point was 0.03) was the only species found in Chajul that was not encountered in Damasco. Golden-crowned Warblers (*Basileuterus culicivor*; 0.01), Thrush-like Manakins (*Schiffornis turdinus*; 0.01), and Long-billed Gnatwrens (*Ramphocaenus rufiventris*; 0.01) all were seen in Damasco but not in Chajul. Other species, such as Orange-billed Sparrows (*Arremon aurantiros-tris*; 0.005), White-breasted Wood-Wren (*Henicorhina leucosticta*; 0.09), and Black-faced Antthrush (*Formicarius analis*; 0.005), occurred in both areas.

Of the 35 most common species of forest residents (based on point counts from forest at Chajul and Bonampak), the only species that appear on the list of common residents (Table 3) are Rufous-tailed Hummingbird (*Amazilia tzacatl*), Little Hermit (*Phaethornis longuemareus*), Spot-breasted Wren (*Thryothorus maculipectus*), Red-throated Ant-Tanager (*Habia fuscicauda*), and Yellow-billed Cacique (*Amblycercus holosericeus*). Although none of the species show a significant difference in abundance between Chajul and Damasco, four of five were recorded at a nonsignificantly higher value in the Chajul region.

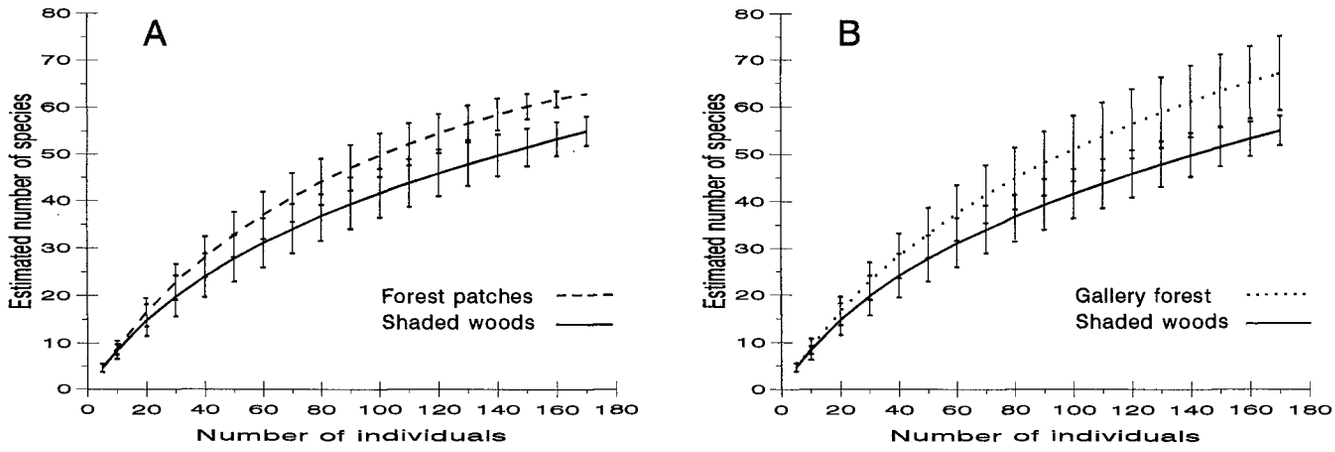

Figure 3. Rarefaction analyses comparing the number of species accumulated and 95% confidence interval for shaded woods habitat with those in forest patches from the Chajul study area, which separate at 130 individuals (a) and in gallery forest from the Damasco study area, which separate at 160 individuals (b).

Comparison of Common Migratory Species

Both areas had similar lists of common migrants (Table 3). Significant differences in abundance occurred for Yellow and Wilson's Warblers, Yellow-bellied Flycatchers, Orchard Orioles, and Tennessee Warblers, which were more common in Chajul, and American Redstart (*Setophaga ruticilla*), Magnolia Warbler, Common Yellow-throat, and Northern Waterthrush, which were more common in Damasco. In general, the same species that were more common in one region for gallery woods were also more common for scrub habitats.

Discussion

Bird Populations in Gallery Woods

Gallery woods habitat contains a high diversity and abundance of birds, but particularly of Nearctic migrants. We found that approximately one-quarter of the species and 40% of the individuals detected were migrants, which is similar to values obtained for other studies in the region (Waide 1980; Lynch 1989; Kricher & David 1992). It is harder to compare absolute numbers, but the value of 4–5 migrants per point (within 25 m) is one of the highest found for all of the 17 habitats surveyed in eastern Chiapas (Greenberg et al., unpublished manuscript), behind only shade coffee plantation and acacia woodlots.

The resident avifauna is dominated by generalist and forest-edge species, such as Spot-breasted Wren, Crimson-collared and Golden-masked Tanagers, Yellow-throated Euphonia, and Red-throated Ant-Tanager. We found a small number of forest-specialized species, even in the arroyo vegetation in the Damasco region. The study was conducted in the nonbreeding season for most species, and it is unknown to what degree these individuals were wanderers from forested areas.

Despite differences in the availability of forested habitat between the two areas examined, overall densities of both migrants and residents were similar for Chajul, which had been cleared 10 years prior to the censuses, and the Damasco study area, which had been cleared as long as 35 years previously (Table 2). The similarity in overall density suggests that, on the broadest level of comparison, there is no "packing" of habitat as the surrounding vegetation is eliminated.

This general similarity masks some potentially interesting differences in abundance that deserve further investigation. As might be expected, one pervasive difference between gallery woods of the two regions is the greater proportion of forest specialists found near Chajul when compared with the proportion seen in the Damasco area (Table 4). Particularly among migrants, there were significantly higher densities of broad generalist species sampled in the Damasco study area (Table 3). But considering the proximity of most of the point counts in the Chajul area to intact forest (most were within 1 km), the number of common forest species was surprisingly low. This suggests that the loss of most of the diversity of tropical forest species occurs early in the clearing process and does not decline much with further clearing.

For several common migratory species, the numbers differed between the regions in ways that invite further investigation. For example, the two most common forest-generalist species (species that are more common in forest but occur in scrub habitats), Magnolia Warbler (*Dendroica magnolia*) and American Redstart, were substantially and significantly more common in the Damasco region than in Chajul. This is apparently not a difference in overall regional winter distribution, because these species were found in similar numbers in the forests adjacent to the two regions (Sterling & Greenberg, in preparation). One possible explanation for the difference in abundance of these two species is

Table 4. Habitat breadth analysis summary for species detected in the six arroyo habitats censused in the two study areas.

	Damasco		*Chajul*			
*Habitat Preference**	*Gallery*	*Scrub*	*Gallery*	*Forest*	*Shade*	*Scrub*
Twenty Most Abundant Species						
Broad Generalists	5 (4)	5 (4)	3 (2)	3 (3)	4 (3)	4 (2)
Moderate Specialists						
pasture/forest patches	12 (6)	12 (5)	8 (2)	6 (3)	4 (1)	11 (5)
forest/forest patches	2	1	3	4	3	2
Specialists						
forest	1	0	1 (1)	4 (3)	2 (1)	2
forest patches	0	0	1 (1)	1 (1)	1 (1)	1
pasture	0	0	0	0	0	0
Not Classified	0	2	4 (1)	2	6	1
Species Ranked 21–40 Based on Abundance						
Broad Generalists	2 (1)	0	3 (3)	2 (1)	1	1 (1)
Moderate Specialists						
pasture/forest patches	3 (1)	7 (3)	5 (3)	6 (2)	4	6 (1)
forest/forest patches	6 (1)	4 (1)	5 (1)	4	3 (1)	4 (1)
Specialists						
forest	1	1	2	3 (1)	3 (1)	5
forest patches	0	1 (1)	0	0	0	0
pasture	0	0	0	0	0	0
Not Classified	8 (2)	7 (1)	5 (1)	5	9 (2)	4 (1)

*Values presented are total number of species in each category (with number of migrants species presented in parentheses) for the 20 most common species and the subsequent 20 most common species. Based upon an independent data set, species were classified as broad generalists; moderate specialists in pasture and forest patches; moderate specialists in broadleaf forest and forest patches; specialists in either broadleaf forest, pasture, or forest patches; or not classified.

the difference in abundance of Yellow Warblers. Yellow Warblers are significantly more abundant in the Chajul arroyos. They are aggressively dominant to Magnolia Warblers and American Redstarts, continually driving them into the less productive understory vegetation (Greenberg & Salgado Ortiz 1994).

Management and Conservation of Arroyo Vegetation

Differences in how arroyo vegetation is managed are pronounced and may have a larger impact on the diversity and abundance of birds than does the overall age or degree of clearing of the surrounding area. The best example of this is shade woods, where the understory is cleared to provide cattle access to the stream and a protected resting area. Shade woods had a significantly lower diversity of birds per point, as estimated by rarefaction analysis, than did other arroyo vegetation types.

The heavy use of arroyo vegetation by migratory birds is typical of second-growth woody vegetation in the region. Some authors have argued that because almost all migrant species are known to use secondary vegetation and because they may achieve high densities in these habitats, forest clearing may not be a problem. We note that in areas of the Lacandon region where cattle pasture is the dominant land use, secondary wooded vegetation is highly restricted in its distribution. Thus, these areas of arroyo vegetation probably support high densities of migratory birds, even compared to other second-growth habitats, because of their location on productive alluvial soils. These high densities are therefore likely a compensation for the fact that, because they tend to be restricted to stream sides, the habitat covers a very small area.

A point of caution is that the high abundance of many migrant species may obscure poor individual success in over-winter survival. Rappole et al. (1989) compared the survival of wintering Wood Thrush in primary and secondary forests and found that survivorship in secondary habitats was significantly lower. Probably because of its dependence on humid undergrowth conditions, Wood Thrush is the forest-migrant species most sensitive to forest loss in the Lacandon region. Many of the common migrants, such as Magnolia Warbler and American Redstart, use wooded vegetation but are not specialized on humid forest. Studies of over-winter survivorship should be directed toward these species. Although detailed studies of the demography and social systems of most migratory species have not been conducted, we have monitored the changes in abundance throughout the winter in forest and gallery woods habitat and found no significant difference in the rate of seasonal decline in forest migrants between the habitats (Salgado Ortiz 1993).

Although the protection of trees along stream courses in cleared areas is commonplace, it cannot be taken for granted. Whereas all of the arroyos in the Chajul region

either retain original forest elements or support secondary scrub or woods, as much as 60% of the stream banks in the Damasco region lack any trees or tall shrubs.

Conclusions

Arroyo woods support a bird assemblage that is considerably degraded from that of the original forest covering the area. The presence of wooded vegetation supports a density and diversity of migratory birds, however, and increases the diversity of resident birds. In particular, arroyo vegetation provides habitat for birds characteristic of secondary habitats that still depend upon arboreous vegetation. The greatest change in the avifauna appears to occur shortly after clearing. We detected few major differences between arroyo vegetation in older, more cleared landscapes. The number of birds supported along arroyos probably depends upon the amount of woody vegetation left. Promotion of the already common practice of protecting arroyo vegetation should benefit migratory bird populations and certain resident populations and should provide additional long-term environmental benefits, such as reduced soil erosion and improved water quality.

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Literature Cited

Browder, J. O. 1993. Tropical forest fragments: colonists' patterns and policy options. Pages 53-55 in J. K. Doyle and J. Schelhas, editors. Forest remnants in the tropical landscape: benefits and policy implications. Smithsonian Migratory Bird Center, Washington, D.C.

Calleros, G., and F. A. Brauer. 1983. Problemática regional de la Selva Lacandona. Dirección General de Dessarrollo Forestal, Secretaría de Agricultura y Recursos Hidraúlicos. Coordinación Ejecutiva del Programa Ecológico de la Selva Lacondona. Palenque, Chiapas, México.

De Vos, J. 1988. Viajes al desierta de la soledad: cuando la Selva Lacandona aún era selva. Secretaría de Educación Pública. México, D.F.

Garcia, G. 1988. Normas de ordenamiento ambiental por actividades y sectores productivos en La Selva Lacandona. Secretaría de Desarrollo Urbano y Ecología, México, D.F.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. Pages 273-286 in J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Greenberg, R., and J. Salgado Ortiz. 1995. Interspecific defense of pasture trees by wintering Yellow Warblers. Auk **III**:672-682.

Hutto, R. L. 1980. Winter habitat distribution of migratory land birds in western Mexico with special reference to small, foliage-gleaning insectivores. Pages 181-203 in A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, D.C.

James, F.C., and S. Rathbun. 1981. Rarefaction, relative abundance, and diversity of avian committee. Auk **98**:785-800.

Janzen, J. H. 1988. Management of habitat fragments in a tropical dry forest: growth. Annals of the Missouri Botanical Gardens **75**:105-116.

Kricher, J. C., and W. E. Davis. 1992. Patterns of avian species richness in disturbed and undisturbed habitats in Belize. Pages 240-246 in J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

Lynch, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan peninsula. 1. General patterns of occurrence. Condor **91**:515-544.

Powell, G. V. N., J. H. Rappole, and S. A. Sader. 1992. Neotropical migrant landbird use of lowland Atlantic habitats in Costa Rica: A test of remote sensing for identification of habitat. Pages 287-298 in J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Rappole, J. H., M. A. Ramos, and K. Winkler. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. Auk **106**: 402-410.

Robbins, C. S., B. A. Dowell, D. K. Dawson, J. A. Colon, R. Estrada, A. Sutton, R. Sutton, and D. Weyer. 1992. Comparison of neotropical migrant landbird populations wintering in tropical forest, isolated forest fragments, and agricultural habitats. Pages 207-220 in J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Salgado Ortiz, J. 1993. Utilizacion de mancones de vegetacion secundaria en areas de agostadero por una comunidad de aves. Tesis profesional. Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

SAS Institute, Inc., 1989. SAS/STAT User's guide, version 6. SAS Institute, Inc., Cary, North Carolina.

Simberloff, D. 1978. Use of rarefaction and related methods in ecology. Pages 150-165 in K. L. Dickson, J. Cairns, and R. J. Livingston, editors. Biological data in water pollution assessment: quantitative and statistical analyses. Special technical publication 62. American Society for Testing and Materials, Philadelphia.

Villaseñor, J. F. 1993. The importance of agricultural border strips in the consevation of North American migratory landbirds in Western Mexico. M.A. thesis. University of Montana, Missoula.

Waide, R. B. 1980. Resource partitioning between migrant and resident birds: the use of irregular resources. Pages 337-352 in A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, D.C.

Whitmore, T. C., and J. A. Sayer. 1992. Deforestation and species extinction in tropical moist forests. Pages 1-14 in T. C. Whitmore and J. A. Sayer, editors. Tropical deforestation and species extinction. Chapman and Hall, London.

World Resources Institute. 1992. World Resources 1992-93. Oxford University Press, New York.