

Bird Populations in Shade and Sun Coffee Plantations in Central Guatemala

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Abstract: *We studied the avifauna of sun and shade coffee plantations and associated mid-elevation habitats during the dry season of 1995. The three plantation types (Inga, Gliricidia, and sun) showed high faunistic similarities with each other and were both distinct and depauperate compared to matorral and forest patch habitats. Of all the coffee plantation habitats, Inga shade had the highest diversity. Species associated with wooded vegetation were more common in shade plantations, particularly in Inga. A second census showed a decline in bird numbers that was more pronounced in sun and Gliricidia than in Inga plantations. Overall, differences between the plantation types were small and all coffee plantations were less diverse than traditional coffee farms previously studied in nearby Chiapas, México. The relatively low bird diversity was probably due to the low stature, low tree species diversity, and heavy pruning of the canopy. These features reflect management practices that are common throughout Latin America. The most common species of birds in all coffee plantation habitats were common second-growth or edge species; more specialized forest species were almost completely absent from plantations. Furthermore, many common matorral species were rare or absent from coffee plantations, even sun plantations with which matorral shares a similar superficial structure. Coffee plantations probably will only be important for avian diversity if a tall, taxonomically and structurally diverse canopy is maintained. We suggest this is most likely to occur on farms that are managed for a variety of products rather than those designated entirely for the production of coffee.*

Poblaciones de Aves en Plantaciones Cafetaleras en Sombra y Sol en la Región Central de Guatemala

Resumen: *Estudiamos la avifauna de plantaciones de café en sol y sombra y los hábitats asociados de elevación media durante la temporada de seca de 1995. Los tres tipos de plantaciones (Inga, Gliricidia y de sol) mostraron una alta similitud faunística y fueron tanto distintivas como pobres comparadas con los hábitats de matorral y parches boscosos. De todas los hábitats de plantaciones de café, el sombreado con Inga tuvo la diversidad mas alta. Las especies mas comunes encontradas en las plantaciones sombreadas fueron especies asociadas con vegetación con maderas, particularmente en plantaciones con Inga. Un segundo censo mostró una disminución en el número de aves, el cual fue mas pronunciado en plantaciones con sol, y sombreadas con Gliricidia que en aquellas con Inga. En general, las diferencias entre los tipos de plantaciones fueron pequeñas y todas las plantaciones de café fueron menos diversas que las plantaciones tradicionales de café estudiadas con anterioridad en los alrededores de Chiapas, México. La relativamente baja diversidad de aves probablemente se debe a la baja estatura, baja diversidad de especies de árboles y a un intenso corte de la copa de los árboles. Estas características reflejan prácticas de manejo comunes a lo largo de toda América Latina. Las especies de aves mas comunes en todos los hábitats de las plantaciones de café fueron especies de segundo-crecimiento o de borde. Especies mas especialistas de bosque estuvieron casi completamente ausentes de las plantaciones. Aunado a esto, muchas especies comunes a matorrales fueron raras o ausentes en los cafetales, aún en las plantaciones de sol con las cuales los matorrales comparten una estructura superficial similar. Los cafetales probablemente serán importantes para la diversidad de aves, si se mantiene una cobertura arborea alta y diversa tanto taxonómicamente como estructuralmente. Sugerimos que esto mas bien podría*

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ocurrir en terrenos que son manejados con diversos productos que en aquellos designados exclusivamente para la producción de café.

Introduction

As more land is converted from natural vegetation to farms and pasture, the role of agroecosystems in conserving biological diversity is receiving more attention (Pimentel et al. 1992). Agricultural systems that incorporate trees, which provide increased structural complexity and resources, are often considered the most benign in their impact on forest organisms. By virtue of its tremendous economic importance for many tropical countries and its traditional use of a tree canopy, coffee has been the focus of considerable research on its potential value as a refuge for organisms that might otherwise be displaced. Ornithologists in particular note the diversity and abundance of birds—especially temperate-tropical migratory species—in shade coffee plantations (Griscom 1932). A few studies have supported the importance of some shade coffee plantations for the conservation of forest birds (Aguilar-Ortiz 1982; Robbins et al. 1992; Wunderle & Waide 1993; Vannini 1994; Greenberg et al., in press; Wunderle & Latta 1996) and other aspects of biological diversity (Nestel et al. 1993; Perfecto & Vandermeer 1994; Perfecto et al. 1996).

Much of what was formerly shade coffee plantation has been converted into sun plantation, where most or all of the canopy trees are removed (Rice 1993). This cultivation system combined with increased inputs of agrochemicals is able to produce much higher yields of coffee. Sun coffee plantations lack the canopy trees that distinguish this crop from many other land use alternatives, and the rapid spread of this system is a matter of concern for the future of biodiversity in coffee plantations (Borrero 1986; Gallina et al. 1992; Wunderle & Latta 1996). However, there is a danger in adopting a dichotomous sun-versus-shade classification in studying the impact of coffee cultivation because the shade canopy of coffee plantations is managed in a variety of ways (Fuentes-Flores 1982). It is entirely possible that there is as much or more variation in the habitat quality of different shade coffee plantations as there is between sun and shade coffee as classes. For example, some coffee is grown under a modified forest cover (rustic plantations) or a tall and diverse planted canopy (traditional mixed plantations). However, these techniques are often characteristic of marginal coffee growing areas. In more established coffee “zones,” where coffee holdings often form large continuous tracts of habitat, it is common to see highly managed shade plantations. These plantations are characterized by a monospecific shade of short-stat-

ure trees (*Inga* spp., *Gliricidia sepium*, and *Erythrina* spp.). Trees are usually trimmed twice each year to maintain a parasol architecture that casts a monolayer of shade (Sanchez Castillo 1994) and to avoid too much humidity, which is believed to promote fungal disease.

Greenberg et al. (in press) reported on the high diversity of birds associated with traditional mixed and rustic plantations in eastern Chiapas. Here we report on a study in the Polochic Valley, north of the Sierra de las Minas in Guatemala. We examined the diversity and seasonal change in abundance of bird populations associated with sun coffee and plantations with managed shade consisting primarily of *Inga* and *Gliricidia*. In addition, we compare these plantation types to matorral (secondary succession from corn fields), rustic cardamom (*Elettaria cardamomum*) plantations, and isolated forest remnants in the same elevational band as the coffee zone.

Study Sites

The study was conducted in the foothills of the Sierra de las Minas in the Polochic Valley (Departamento de Alta Verapaz). Bird surveys were conducted at four sites located along a 60-km transect of the Polochic Valley. The location and elevational range at each site are listed from west to east as follows: Tamahú (15° 8'N, 90° 14'W; 674–1818 m), Tukurú (15° 8'N, 90° 7'W; 389–1455 m), Jolomjix (15° 16'N, 89° 45'W; 262–665 m), and Pueblo Viejo (15° 18'N, 89° 41'W; 221–747 m). The natural vegetation ranges from lowland moist tropical forest to pre-montane forest and pine-oak woodlands. We studied three types of coffee plantations classified by their dominant shade management: *Inga* shade, *Gliricidia* shade, and sun. *Inga* shade grows at higher elevations than *Gliricidia*, whereas sun plantations can be found throughout the elevational gradient. The shade of both plantation types is dominated by the genus or species for which they are named. However, over 45 species of trees were found in the *Inga* and 29 in the *Gliricidia* plantations. Both shade plantation types are characterized by a low (6–8 m) and relatively open (40–50% cover) canopy (Table 1). *Gliricidia* plantations are strongly dominated (85%) by the most common tree (vs. 61% for *Inga*) and show considerably lower vertical structural complexity compared to *Inga* plantations (within-point Coefficient of Variation [CV] of tree height = 11% versus 20%, respectively). In

areas of sun plantations that have trees, the trees are small (5–6 m) and the canopy cover negligible. There is an elevational gradient in dominant leaf size of the shade trees, with the lowest elevation using small-leaved *Gliricidia*, mid-elevation using the small-leaved *I. spuria* and the medium-leaved *I. edulis*, and the highest plantations using mostly the large-leaved *I. micheliana*. The period from January to April is one of marked phenological change. Two of the common *Inga* species (*I. spuria* and *I. edulis*) produce a profusion of flowers from mid-March on. *Gliricidia* flowers in January and loses its leaves from late January to mid- to late March (depending on elevation). Our first census period coincided with the flowering of *Gliricidia* and the second spanned the beginning and peak of flowering for *Inga* and the leafing out of *Gliricidia*. In addition to these natural rhythms, shade trees were heavily pruned in approximately half the plantations between the two census periods, substantially reducing shade cover.

For comparative purposes we surveyed matorral, forest remnants, and rustic shade cardamom plantations. Matorral was secondary shrubbery, usually generated by succession from corn fields. Forest remnants were small patches of forest ranging from 1 to 10 ha. Rustic cardamom consisted of an understory of cardamom and a canopy of secondary tropical forest species. We considered cardamom the closest habitat to secondary, low elevation forest remaining in the areas. Because the coffee plantations were surveyed at a variety of elevations and elevation is an important variable governing bird community composition, we surveyed the matorral and forest habitats along the same elevational gradient in which coffee was found. Matorral was surveyed at low and high elevation sites; forest remnants were surveyed at high elevation sites; and cardamom was surveyed primarily at low elevation sites.

Methods

Bird census data are based on fixed-radius point counts (Hutto et al. 1986; Petit et al. 1994). Counts were made in a total of 666, 25-m fixed-radius plots. Most counts in coffee plantations and matorral were surveyed twice: once in period I (January–February 1995) and again in period II (mid-March–mid-April). Forest habitats were surveyed only once during the study. Each point was surveyed for 10 min from 0645–1000; therefore, nocturnal birds are not included in these analyses. Points were located at least 25 m from the edge of the woodlots and 200 m from the nearest point. All birds within 25 m were recorded. Points were located along approximately 2-km transects which were established as much as possible within a single drainage and elevation zone. We excluded individuals that were flying over the point. Whenever possible, the observer recorded the type of shrub or tree in which the bird was located. These data were used to assess the relative use of the coffee versus canopy layer. In addition, the surveyor recorded the elevation (based on altimeter readings), number of trees, the estimated canopy height and the areal extent of the plantation, the number of tree morphospecies, and the average coffee plant height for the 25-m-radius circle. The height and flowering or fruiting status of each tree was also recorded.

Not all habitats were present at each of the four sites. We made every effort to distribute the point count transects as widely as possible in the study area. Because of this we surveyed virtually all of the available habitat accessible from the main roads in the Polochic Valley. The distribution of the number of points for each habitat is as follows: sun coffee (28 points in Pueblo Viejo, 82 in Tucurú); *Inga* (122 Tamahú, 82 Tucurú); *Gliricidia* (25 Jolomjix, 80 Tucurú); matorral (20 Pueblo Viejo, 57 Tu-

Table 1. Descriptive statistics for habitats surveyed based on estimates made at point count circles.^a

Habitat	N	Elevation (m)	Canopy cover (%)		Tree species	Tree/ba	\bar{X} tree height (m)	SD tree height ^b (m)	Dominance (%) ^c	Coffee cover (%)
			Period I	II						
<i>Inga</i>	204	786 (197) 369–1185 ^d	50 (18)	39 (19)	3.8 (1.7)	153 (71)	6.9 (1.4)	1.38 (1.15)	60 (6)	66 (20)
<i>Gliricidia</i>	102	447 (99) 102–692	35 (14)	40 (15)	3.7 (2.2)	245 (82)	6.7 (1.0)	0.77 (0.66)	83 (17)	65 (25)
Sun	104	646 (243) 262–1231	7 (7)	5 (7)	2.8 (1.5)	66 (33)	4.7 (1.4)	0.74 (1.05)	55 (37)	68 (21)
Matorral	77	497 (186) 200–862	—	—	2.2 (1.9)	33 (28)	4.7 (2.87)	0.68 (1.12)		
Forest Remnant	71	1088 (252) 707–1723	78.7 (19)		18.2 (17.8)	267 (103)	13.0 (4.77)	3.99 (1.97)		
Rustic Cardamom	101	778 (342) 392–1378	68.8 (13)		9.5 (4.4)	144 (51)	13.8 (5.44)	3.71 (1.82)		

^aMean with standard deviation in parentheses.

^bWithin point standard deviation of tree height.

^cTree dominance: the number of *Inga* or *Gliricidia*/the number of total trees.

^dElevation Range.

curú), shade cardamom (55 Pueblo Viejo, 46 Tukurú), forest remnant (50 Tamahú, 21 Tukurú).

For species richness we present the total number of species recorded on point counts for a habitat. To bring the large (204 points) *Inga* sample into line with the other habitats, we randomly selected 106 points. To control for different sampling effort, we conducted a rarefaction analysis (James & Rathbun 1981). We compared the expected number of species with a sample of 400 individuals.

We estimated overall faunal similarities using the index of Dice (1945): $2a/2a + b + c$, where a is the number of shared species and b and c are the numbers of unique species in the two habitats. These values were clustered (Wilkinson 1990) using the single-linkage nearest-neighbor method based on Euclidean distance. The calculations are based on the first census period for coffee plantations.

To examine variation in the abundance of total birds, residents, migrants, and common species (>0.10 /points for at least one habitat), we conducted a two-way ANOVA for habitat and between-period variation. To avoid basing our analysis on replication over too small an area, we used the mean number of individuals observed over all the points in a single transect. At other locations where plantations are small and isolated (Greenberg et al. in press), we pooled data for individual plantations. However, at the Polochic Valley site the plantations were large, interconnected, and encompassed tremendous underlying diversity in elevation and other site characteristics. The average amount of area in coffee for the 12 plantations we worked on was 320 ha (range 26–1000 ha), which is far larger than the national average of 8.7 ha for Guatemala (ANACAFE, unpublished data). At the Tamahú site coffee was managed in a communal zone, rather than discrete holdings.

We classified species based on whether they were found more abundant on the natural shade cardamom and forest remnant (woodland species) or the matorral (shrub species) point counts. We refer to species as woodland rather than forest species because, although we found species in coffee plantations that are common in patches of woods, almost none are species that would be associated with large forest tracts.

To detect patterns among a larger group of species that included those with smaller sample sizes (and so individually may not show significant habitat variation), we ranked the three coffee habitats by the average number of individuals seen per point for species in each class. A mean ranking close to 1 would indicate that a plantation type supports the greatest number of individuals for most species for that habitat class. Similarly, a mean rank close to 3 would indicate the lowest abundances. We tested the differences in rankings between habitats with a Kruskal-Wallis test.

The above analyses only test for differences between plantation types. However, because of potentially con-

founding variables (such as elevation), they cannot establish with certainty the role of shade management. In order to tease apart the role of different habitat variables we entered habitat variables into a multiple regression (SAS 1989) with bird number per point as the dependent variable. Because many of the habitat parameters varied considerably between adjacent points, we have conducted the regression analysis on a per point rather than a per transect basis. The variables included: elevation, distance to edge of plantation, total trees, tree species, percentage of trees of the dominant type (*Inga* or *Gliricidia*), the mean height of all trees, coefficient of variation of height of trees (as an index of vertical complexity), shade cover, and coffee cover. First, the scatter diagrams for all habitat variables versus bird abundance were examined for obvious, interpretable non-linear patterns. Finding none, variables were then entered into a step-wise multiple linear regression (forward selection). We considered significant all variables that were entered into the regression equation, which were then tested with a student's *t*-test based on the regression coefficient divided by its standard error.

Because in other regions we have found that the flowering of *Inga* attracts large numbers of nectarivorous or omnivorous species (Greenberg et al. in press), we conducted focal watches totaling 27 hours at nine different patches of flowering *Inga edulis* between 22 March and 1 April. We present the total number of visits by different species as an indication of how *Inga* flowers are used by the bird community in this region.

Results

Species Richness

For habitats sampled with approximately the same number of points, the highest number of species was recorded in the forest habitats (87–122), followed by *Inga* coffee (73), then *Gliricidia* and sun coffee (approx. 65, see Table 2). We recorded approximately the same number of species on matorral points as on *Inga* coffee with a smaller sampling effort (70 points). A similar pattern was found in habitats surveyed in the second period, although the number of species recorded was lower in all habitats.

The number of migrant species was similar among habitats (23–29), but there was considerable variation in the number of resident species: *Inga* had 48, compared to 38 for *Gliricidia* and 40 for sun in period I, and *Inga* had 42, compared to 33 for both sun and *Gliricidia* in period II. *Inga* was similar to matorral (47 and 43 species in periods I and II) and considerably lower than forest and cardamom (63 and 93, respectively).

When only regular species are considered (>0.05 individuals/point, Table 3), coffee plantations had 18–26

Table 2. Total species richness and number of species expected in samples of 400 individuals (based on rarefaction analysis) for habitats sampled in period I (Jan.–Feb.) and period II (Mar.–Apr.).

Habitat*	Period I		Period II	
	Total	Estimated (SD)	Total	Estimated (SD)
<i>Inga</i> (108, 106)	73	62.1 (3.2)	65	55.5 (3.1)
<i>Gliricidia</i> (103, 102)	64	58.1 (2.0)	53	46.3 (0.8)
Sun (110, 110)	65	58.7 (1.6)	55	49.2 (1.2)
Matorral (77, 56)	70	64.3 (2.0)	63	61.2 (1.2)
Forest Remnant (71)			87	72.2 (2.3)
Cardamom (101)	122	95.3 (2.1)		

*Numbers refer to number of points surveyed. Where there are two numbers, they refer to period I and II respectively.

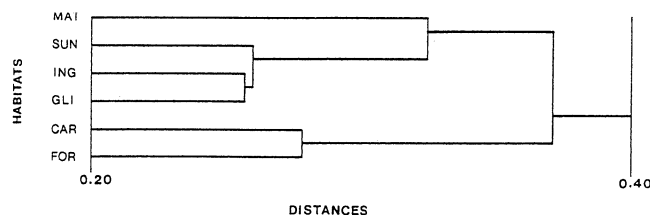
species (migrants plus residents) in period I compared to 33 species in matorral, 43 species in remnant, and 53 species in cardamom. This pattern is similar in period II, with a disproportionate reduction in species in *Gliricidia*. Again, most of the variation is found in the resident species totals.

The rarefaction analysis provided a similar pattern to the one found in total counts (Table 2): forests had the highest density, followed by matorral, *Inga* coffee, then sun and *Gliricidia*. However, the differences were generally small, particularly between the coffee plantations and matorral.

Faunal Similarities and Bird Abundance

The three coffee plantations clustered together, with matorral as their nearest habitat outgroup. The two "forest" habitats, remnant and cardamom, clustered together (Fig. 1).

The abundance of migratory birds was generally similar between the three Polochic Valley coffee plantation habitats (Table 3). However, there was a marked difference in the degree to which migrants declined between periods, with *Gliricidia* losing 50% of its individuals. The seasonal decline was only 20% and 5% for *Inga* and sun, respectively. A two-way ANOVA (habitat versus period) produced a significant period effect ($F_{1,81} = 8.4, p =$

**Figure 1.** Cluster analysis, based on Dice's Similarity Index, of habitats surveyed in the Polochic Valley, Guatemala. Habitat acronyms are Mat, Matorral; Sun, Sun; Ing, *Inga* coffee; Gli, *Gliricidia* coffee; Car, shade cardamom; and for, forest remnant.

0.005). Resident numbers differed significantly between habitats ($F_{2,81} = 6.3, p = 0.005$). *Inga* coffee had significantly more birds than sun coffee, based on a Bonferroni post-hoc comparison. Finally, total birds per point showed a significant habitat ($F_{1,81} = 5.6, p = 0.005$) and a nearly significant period effect ($F_{1,81} = 3.5, p = 0.06$), with *Inga* having significantly more birds than sun coffee, and the early season having more birds than the later season.

Individual Species

The common forest migrant species (including species recorded at an abundance >0.10 per point in at least one plantation type; see Table 4 for habitat classification) showed a consistently significant variation in abundance between the coffee plantation types based on a two-way ANOVA of habitat versus period (df = 2,81 for all between-habitat comparisons). Four of the 5 species were most common in *Inga*: Yellow-bellied Flycatcher ($F = 5.9, p = 0.004$), Wood Thrush ($F = 2.9, p = 0.06$), Tennessee Warbler ($F = 3.8, p = 0.026$), and Black-throated Green Warbler ($F = 8.5, p < 0.001$). Blue-gray Gnatcatcher was most common in *Gliricidia* ($F = 4.5, p = 0.012$). The scrub species also showed significant habitat variation, with 4 of 6 most common in *Gliricidia*: Ruby-throated Hummingbird ($F = 18.6, p < 0.001$), Least Flycatcher ($F = 13.8, p < 0.001$), Yellow Warbler ($F = 8.4, p < 0.001$), and Magnolia Warbler ($F = 22.3, p < 0.001$). Wilson's Warbler ($F = 8.8, p < 0.001$) and Indigo

Table 3. Total number of species (TSp), total common species (CSp, >0.05 ind. per point), and average number of individual (Ind) migrant and resident species per point for both periods.

Habitat	Period I						Period II					
	Migrant			Resident			Migrant			Resident		
	TSp	CSp	Ind	TSp	CSp	Ind	TSp	CSp	Ind	TSp	CSp	Ind
<i>Inga</i>	29	9	2.5	48	9	3.1	23	6	2.0	42	12	3.2
<i>Gliricidia</i>	25	13	3.2	38	13	2.4	20	6	1.6	33	13	2.6
Sun	26	9	2.0	40	12	2.4	22	8	1.9	33	9	1.5
Matorral	23	13	3.3	47	20	3.9	20	12	3.0	43	20	4.8
Forest Remnant							23	9	2.9	63	32	5.8
Cardamom	29	16	4.4	93	37	4.9						

Table 4. Mean number of individuals per point of birds (minimum 0.05 ind./point) on point counts in the six major habitats studied.^a

	Inga			Gliricidia			Sun			Matorral			Cardamom ^b	Remnant		
	Period	I	II	I	II	I	II	I	II ^b							
Migrants	Tewa	0.70	0.71	Tewa	0.63	0.43	Wiwa	0.37	0.12	Inbu	0.73	0.50S	Btgw	1.06F	Tewa	0.73
	Btgw	0.52	0.49	Mawa	0.53	0.41	Mawa	0.34	0.29	Grca	0.40	0.36S	Wiwa	0.65F	Wiwa	0.62
	Wiwa	0.33	0.15	Btgw	0.51	0.13	Lefl	0.24	0.10	Coye	0.32	0.50S	Cswa	0.47F	Btgw	0.52
	Mawa	0.18	0.13	Lefl	0.33	0.17	Inbu	0.24	0.75	Wiwa	0.30	0.13S	Tewa	0.44F	Swth	0.27F
	Ybfl	0.16	0.11	Ruth	0.26	0.03	Btgw	0.19	0.11	Lefl	0.26	0.29S	Ybfl	0.39F	Grca	0.21
	Woth	0.13	0.02	Yewa	0.17	0.20	Yewa	0.12	0.07	Mgwa	0.22	0.16S	Amre	0.19F	Oven	0.07
	Inbu	0.08	0.10	Bggn	0.14	0	Tewa	0.10	0.19	Mawa	0.22	0.25S	Howa	0.19F	Woth	0.07
	Howa	0.06	0.01	Wiwa	0.09	0	Cswa	0.06	0.06	Ybch	0.21	0.18S	Woth	0.14	Mawa	0.07
	Grca	0.05	0.03	Gcfl	0.07	0	Oven	0.05	0.03	Oven	0.13	0.20S	Mawa	0.12F	Mgwa	0.06
				Oven	0.07	0.01				Tewa	0.09	0.04	Kewa	0.12F		
				Ybfl	0.07	0.05				Woth	0.08	0.04	Cewa	0.10F		
				Sovi	0.05	0.01				Oror	0.08	0 S	Suta	0.09F		
				Baor	0.05	0				Yewa	0.05	0.05S	Bwwa	0.06F		
										Rbgr	0.01	0.13S	Rbgr	0.06		
										Blgr	0.03	0.07S	Weta	0.05F		
													Bggn	0.05F		
Residents	Mebl	0.53	0.62	Chor	0.41	0.10	Ccro	0.31	0.14	Plwr	0.47	0.46S	Lihe	0.31F	Gcrw	0.54F
	Chor	0.43	0.24	Bhsa	0.28	0.28	Rcwa	0.30	0.24	Bblg	0.36	0.45S	Obeu	0.29F	Wbww	0.51F
	Ccro	0.34	0.36	Mebl	0.26	0.36	Yfgr	0.30	0.11	Ybca	0.26	0.32S	Legr	0.23F	Lihe	0.27
	Bhsa	0.24	0.21	Ccro	0.20	0.45	Bblg	0.24	0.06	Gban	0.22	0.32S	Bcja	0.22F	Cbta	0.27F
	Brja	0.21	0.24	Brja	0.11	0.25	Bhsa	0.20	0.03	Bhsa	0.19	0.23S	Bhsa	0.18	Scso	0.24
	Rcwa	0.20	0.19	Gban	0.10	0.18	Gtgr	0.15	0.03	Rthu	0.18	0.11S	Ccro	0.17F	Obfl	0.24
	Gfwo	0.13	0.21	Yofl	0.12	0.07	Chor	0.14	0.08	Lihe	0.16	0.11	Yofl	0.17F	Chor	0.24
	Rbaz	0.07	0.28	Rthu	0.08	0.08	Mebl	0.12	0.14	Wcse	0.16	0.07S	Btsa	0.15F	Sbwr	0.20F
	Rthu	0.07	0.16	Bbfl	0.06	0	Brja	0.11	0	Rusp	0.16	0.29S	Bheu	0.14F	Rbaz	0.18
	Lihe	0.04	0.07	Bcmo	0.05	0.03	Rthu	0.09	0.06	Ftem	0.14	0.16S	Gfwo	0.13F	Emto	0.18
	Ybor	0.03	0.09	Sofl	0.05	0.01	Wcse	0.07	0.02	Ytor	0.14	0.11S	Mati	0.12F	Bhsa	0.15
	Gtgr	0.03	0.05	Achu	0.05	0.06	Wcpa	0.05	0	Rcwa	0.14	0.41S	Bbwr	0.11F	Mati	0.13
				Gfwo	0.04	0.11	Wfgs	0.04	0.11	Baan	0.10	0.16S	Dcfl	0.09F	Rtat	0.13
				Rcwa	0.03	0.18	Ftem	0	0.07	Sbwr	0.08	0.05	Rbaz	0.09F	Grja	0.13
				Grki	0.02	0.11				Wtdo	0.08	0.02S	Grja	0.09F	Gowo	0.13
				Otpa	0.02	0.08				Ccta	0.06	0 S	Yteu	0.08F	Stre	0.11F
				Rbpi	0	0.06				Otpa	0.06	0.02S	Grho	0.08F	Legr	0.11
										Mebl	0.06	0.27S	Shwo	0.08F	Bcch	0.11
										Ybor	0.06	0.04S	Chor	0.08F	Bheu	0.08
										Plch	0.05	0.07S	Bbfl	0.08F	Ywta	0.08
										Wfgs	0.04	0.27	Bcch	0.07F	Bts	0.07
										Rbaz	0.03	0.09	Coar	0.07F	Yofl	0.07
										Dcfl	0.03	0.09	Fcta	0.07F	Cotr	0.07F
										Brja	0.03	0.07	Rthu	0.07F	Bcmo	0.07
										Chor	0.01	0.13	Ywta	0.07F	Obsp	0.07
										Btsa	0.00	0.05	Mebl	0.07	Ccro	0.07
													Rcwa	0.06	Yteu	0.07
													Emto	0.06F	Blro	0.07
													Ybor	0.06	Dcfl	0.06
													Bcmo	0.06F	Visa	0.06
													Gmta	0.05F	Brat	0.06
													Ccwo	0.05F	Erfl	0.06
													Scfl	0.05F		
													Scso	0.05F		
													Sbwr	0.05		
													Kbto	0.05F		
													Obfl	0.05F		

^aSpecies are listed in order of abundance during period I. See Appendix A for common names, Latin names, and species codes used in this table.^bS = scrub and F = forest.

Bunting ($F = 5.8$, $p = 0.004$) were most common in sun plantations. Overall, 9 of 11 migrant species were most common in one of the shade plantation types. Although migrant abundance showed a significant seasonal decline, only 4 of the 11 species of migrants individually tested showed such a pattern (Wilson's Warbler, Least Flycatcher, Wood Thrush, and Ruby-throated Hummingbird).

Five of the 7 common woodland residents showed significant variation in abundance across plantation types: Golden-fronted Woodpecker ($F = 8.17$, $p = 0.001$), Azure-crowned Hummingbird ($F = 4.5$, $p = 0.014$), Clay-colored Robin ($F = 4.0$, $p = 0.02$), and Chestnut-headed Oropendola ($F = 3.85$, $p = 0.025$) were most common in *Inga* plantations; Yellow-olive Flycatcher ($F = 9.2$, $p < 0.001$) was most common in *Gliricidia*; and Greater Kiskadee and Black-headed Saltator showed no significant habitat-based variation. Only 3 of the 8 common scrub species showed significant habitat variation: Yellow-faced Grassquit ($F = 23.8$, $p < 0.001$) and White-faced Ground Sparrow ($F = 7.93$, $p < 0.001$) were most common in sun plantations; and the Melodious Blackbird ($F = 9.45$, $p < 0.001$) was most common in *Inga* plantations. Rufous-tailed Hummingbird, Groove-billed Ani, Brown Jay, Rufous-capped Warbler, and Great-tailed Grackle showed no significant habitat variation. Only 2 of the 15 resident species analyzed showed significant seasonal declines (Yellow-faced Grassquit, $F = 6.2$, $p < 0.014$, and Yellow-olive Flycatcher, $F = 5.6$, $p = 0.02$).

The broader analysis of habitat rankings based on all species showed a similar pattern to the above single-species tests. There was significant between-plantation-type variation in the ranking of 10 forest migrants (Kruskal-Wallis = 14.7, $p < .001$, see Table 4 for classification and abundance data) during period I, with forest migrants having a mean abundance rank of 1.6 in both *Gliricidia* and *Inga* and 2.8 in sun coffee. The difference between habitats was not significant in period II with mean rankings for 11 species of 1.6, 2.2, and 2.1 for *Inga*, *Gliricidia*, and sun, respectively. The difference between habitats for scrub migrants was not significant. We also found significant variation between habitats in the ranking of forest residents with mean rankings for 17 species of 1.4, 2.1, and 2.6 for *Inga*, *Gliricidia*, and sun coffee during period I ($KW = 21.7$, $p < 0.001$), and 1.3, 2.1, and 2.6 for period II ($KW = 19.0$, $p < 0.001$). Again, the pattern across habitats for scrub species was not significant.

Correlations with Habitat Variables

Bird abundance depends upon the structure and diversity of the canopy: the total number of birds per point was significantly positively related in period I to shade cover, the coefficient of variation of tree height, and the number of tree species and negatively related to elevation and positively related in period II to shade cover,

mean height, and CV of height. The model is highly significant but explains only a small proportion of the total variance ($R^2 = 0.13$ and 0.095 , respectively). Resident birds show a similar pattern ($R^2 = 0.13$ and 0.15 for periods I and II, respectively) with a model based on, for period I, a positive relationship with the CV of tree height, mean tree height, and the number of tree species and a negative relationship with elevation and tree dominance for period II and a positive relationship with mean height, shade cover, and tree species and a negative relationship with tree dominance. The models for migrants are considerably weaker ($R^2 = 0.048$ and 0.022 for periods I and II, respectively). In this case the important variables are shade cover, tree species, and (negative) elevation for period I. Period II deviates from this, with CV of tree height the only variable accepted into the model.

Use of Shade Trees, Coffee Bushes, and Flowering *Inga*

Overall, birds were recorded in shade trees in coffee plantations far more often than in the coffee layer (74%, 2293 observations). Three of the 6 common migrants (those occurring with an abundance of >0.10 in any habitat) and 8 of the 12 residents occurred in canopy trees $>80\%$ of the time. Only Wilson's Warbler, Yellow-faced Grassquit, Blue-black Grassquit, and Rufous-capped Warbler specialized on the coffee layer.

We observed only seven species feeding on *Inga* flowers during our focal observations. Of the 93 observed visits 50% were made by one species of hummingbird (Azure-crowned) and 72.3% were made by two species of hummingbird (adding Rufous-tailed Hummingbird). Other visitors were either hummingbirds or icterids.

Discussion

Inga coffee plantations support slightly higher numbers of birds—and the populations experienced less decline between the early and late dry season—than the other coffee plantation types. In addition, overall diversity was higher. Not surprisingly, coffee plantations were both faunistically distinct and depauperate compared to remnant forest habitats.

Woodland birds, generalist species that occur more commonly in any wooded habitat, were consistently more common in *Inga* than in other plantation types. Almost all of the migratory species showing significant inter-habitat variation in numbers were most common in one of the shade plantation types, with forest species (Wood Thrush, Black-throated Green Warbler, Tennessee Warbler, and Yellow-bellied Flycatcher) found most commonly in *Inga* and scrub-open species found most commonly in *Gliricidia* plantations.

As in previous studies (Wunderle and Latta 1996), the comparisons are necessarily confounded by elevation. However, *Gliricidia* supported a lower diversity of birds (particularly late in the season) than *Inga*, which is a pattern opposite of what would be predicted by general elevational patterns of diversity. All other variables controlled for elevation consistently entered with a negative coefficient in the multiple regression models. In addition, lower elevation sites support more species; this is the case in the forest remnant to cardamom comparison, where the lower elevation cardamom sites had higher diversity than higher elevation forest remnants or cardamom sites. Sun coffee plantations spanned the range of the *Gliricidia* and *Inga* belts and so are probably comparable with shade plantations. The regression analysis showing a positive relationship between bird abundance and variables related to shade cover and diversity suggests that shade management is an important factor explaining differences between plantation types.

Use of the Coffee Layer

There are reasons to suspect that the coffee layer itself is a particularly poor habitat, even in comparison to other single-layered shrubby habitats in tropical areas. First, the coffee layer in sun plantations not only lacks many of the forest or forest edge species that rely upon the canopy layer, but it also does not support many of the most common species of birds found in adjacent areas of matorral. For example, several species most characteristic of scrubby habitats, including the migrant Gray Catbird, Yellow-breasted Chat, and Common Yellowthroat and the resident Plain and Spot-breasted Wrens, Rusty Sparrow and Barred Antshrike, were virtually absent from all coffee plantations. It appears that diversity and density of all birds are substantially higher in matorral than sun coffee. Finally, the common migrants found in the coffee layer (Magnolia and Wilson's Warblers) are socially subordinate to a territorial migrant (Yellow Warbler) which defends small trees in sun plantations interspecifically (Greenberg et al. 1996). The coffee layer provides few resources for omnivorous or granivorous birds (which dominate matorral) because "weeds" are discouraged through the use of herbicides. Coffee itself is an understory plant that is forced to grow in open sunlight. However, it retains many of the physiological and ecological properties of understory plants (Coley et al. 1985), including chemically defended or "tough" leaves (Frischknecht et al. 1986) which may be one of the reasons they support a low density of herbivorous arthropods. In a bird enclosure study conducted contemporaneously with this project, we found arthropod biomass per 100 g leaf biomass was approximately 6 times greater for *Inga* than shade coffee foliage (0.639 g vs. 0.111 g) and over 14 times

greater than sun coffee foliage (0.043 g) (unpublished data).

Ocosingo Area

The results from the plantations in the Polochic Valley contrast markedly with those from the Ocosingo area of Chiapas, only 276 km northwest (Greenberg et al., in press). We observed approximately half the number of birds per point and only two-thirds the species richness in approximately the same number of points (100) at each site. Furthermore, the Guatemalan plantations were almost completely devoid of even the most generalized forest resident species. These differences hold even when we restrict our comparison to *Inga* plantations in the two regions. The Guatemalan plantations had lower numbers of species in most guilds, with the greatest absolute reduction in canopy omnivorous species. Coffee plantations in Ocosingo were most similar to the rustic cardamom plantations in abundance and diversity.

The comparison is potentially confounded by the geographic separation of the regions. Unfortunately, it is difficult to make direct comparisons of more rustic versus more modern plantations because plantations at the extremes of management types are seldom found in the same region. However, because (1) both regions had a similar degree of agricultural development and forest loss; (2) forest remnants in the Polochic Valley contained many of the forest birds missing from the coffee plantations; and (3) the rustic cardamom plantations had numbers of birds per point and diversity similar to the coffee plantations of Ocosingo; it is likely that the lower abundance and diversity of birds in the Guatemalan plantation relate at least partly to the management of the plantations. In contrast to the Guatemalan plantations, the plantations in Ocosingo had tall canopy and diverse stratification (Fig. 2). Furthermore, trimming was rare. Large trees had old limbs that supported mosses, lichens, and epiphytes, which probably supported a number of birds missing from the Guatemalan plantations (woodcreepers, euphonias, etc.). In addition, all of the Guatemalan plantations used insecticides (Siguenza personal communication), a practice which was rare in Ocosingo.

Another large difference was the lack of an influx of nectarivorous, frugivorous, and omnivorous birds—a phenomenon that was striking in the Ocosingo plantations. In particular, we expected some influx of birds with the flowering of *Inga* in the late dry season (Vanini 1994; Greenberg et al. in press). However, rather than increases in migrant abundances in the late dry season, we found a significant pattern of decrease. Only two hummingbird species fed at flowering *Ingas* to any extent. We believe the extensive pruning, which reduces tree size and may affect flowering, may underlie the lack of nectarivores in the Polochic plantations.

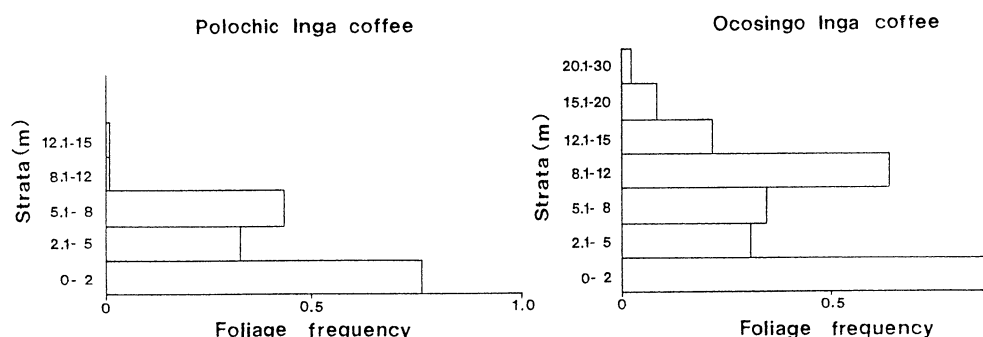


Figure 2. Foliage height profiles based on samples taken on 1-km transects through Inga coffee plantations in the Polochic Valley and the Ocosingo region of eastern Chiapas. Foliage frequency is the number of foliage contacts per point in a given stratum.

Conclusions

Based on surveys of coffee plantations in the Polochic Valley, we conclude that the shade plantations, particularly those dominated by *Inga*, provide habitat for some woodland residents and migrants. These species were less common or missing from sun plantations or those where the shade is dominated by the deciduous *Gliricidia* trees. The number of birds per point, particularly resident birds, was generally related to variables that describe the height and structural diversity of the canopy. Based on comparisons with more forest-like and traditional plantations in Chiapas, Mexico, however, we conclude that the heavy shade management of the Polochic plantations reduces the resources for a substantial number of true forest species. Although the *Inga* shade plantations of the Polochic Valley experience less seasonal reduction in bird populations than the other local plantation types, they do not attract the influx of omnivorous canopy species that characterizes the traditional plantations of Chiapas.

Because of current efforts to bring "biodiversity-friendly" coffee to the marketplace, there is already a move to market coffee produced from shaded plantations which may ultimately increase the area of these types of plantations. In addition, other factors might contribute to the regeneration of shade in "technified" coffee plantations. First, when coffee prices are low, many producers cannot afford the inputs necessary for the continued cultivation of sun coffee and there is regeneration and deliberate planting of shade trees. This apparently occurred during the most recent depression in coffee prices from 1989–1993 (Perfecto personal communication). Second, when coffee is grown in areas of acid soil or with consistently sunny dry seasons, plants suffer from a variety of problems referred to as *mal de viñas* in Guatemala (MacVean et al. 1992). In some areas this has caused a reversion from sun to shade management systems.

Unfortunately, based on our current knowledge of bird use of coffee plantations we would argue that the pres-

ence of shade is only part of the story. The benefits of coffee cultivation to the conservation of biodiversity will only be fully realized if we adhere to generally accepted notions regarding the maintenance of biological diversity.

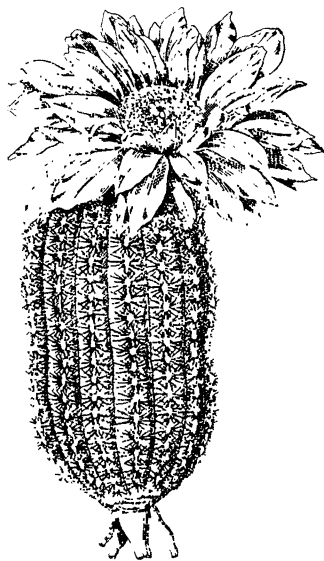
Plantations should have the greatest structural and floristic diversity possible and still allow economically viable returns from a coffee farm. How the potential economic returns of a coffee farm are framed may be critical to the issue of shade management. To a large degree coffee farmers manage shade to maximize coffee production. If this is the only goal of shade management, then the planting of a monospecific canopy and subsequent shade management through continued heavy pruning is a reasonable approach (Beer 1987). However, a structurally and taxonomically diverse canopy can be beneficial for farmers that manage their plantation to be an economically diverse agroforestry system. The promotion of such systems will lessen the dependence of small farmers on a single cash crop and have the secondary effect of improving coffee farms as habitat for birds and other organisms.

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Appendix A

Species code, common name, genus and species, and migratory status of birds encountered in the habitats studied.

Code	Common Name	Genus and Species	Status*
Plch	Plain Cachalaca	<i>Ortalis vetula</i>	R
Rbpi	Red-billed Pigeon	<i>Columba flavirostris</i>	R
Wtdo	White-tipped Dove	<i>Leptotila verreauxi</i>	R
Otpa	Olive-throated Parakeet	<i>Aratinga astec</i>	R
Wcpa	White-crowned Parrot	<i>Pionus senilis</i>	R
Gban	Groove-billed Ani	<i>Crotophaga sulcirostris</i>	R
Lihe	Little Hermit	<i>Phaethornis longuemareus</i>	R
Visa	Violet Sabrewing	<i>Campylopterus hemileucurus</i>	R
Ftem	Fork-tailed Emerald	<i>Chlorostilbon canivetii</i>	R
Rthu	Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	R
Achu	Azure-crowned Hummingbird	<i>Amazilia cyanocephala</i>	R
Ruth	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	M
Cotr	Collared Trogon	<i>Trogon collaris</i>	R
Bcmo	Blue-crowned Motmot	<i>Momotus momota</i>	R
Emto	Emerald Toucanet	<i>Aulacorhynchus prasinus</i>	R
Coar	Collared Aracari	<i>Pteroglossus torquatus</i>	R
Kbto	Keel-billed Toucan	<i>Ramphastos sulfuratus</i>	R
Gfwo	Golden-fronted Woodpecker	<i>Melanerpes aurifrons</i>	R
Gowo	Golden-olive Woodpecker	<i>Piculus rubiginosus</i>	R
Ccwo	Chestnut-colored Woodpecker	<i>Celeus castaneus</i>	R
Shwo	Streak-headed Woodcreeper	<i>Lepidocolaptes souleyetii</i>	R
Baan	Barred Antshrike	<i>Thamnophilus doliatus</i>	R
Obfl	Ochre-bellied Flycatcher	<i>Mionectes oleagineus</i>	R
Scfl	Sepia-capped Flycatcher	<i>Leptopogon amaurocephalus</i>	R
Erfl	Eye-ringed Flatbill	<i>Rhynchocyclus brevirostris</i>	R
Yofl	Yellow-olive Flycatcher	<i>Tolmomyias sulphureus</i>	R
Ybfl	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	M
Lefl	Least Flycatcher	<i>Empidonax minimus</i>	M
Brat	Bright-rumped Attila	<i>Attila spadiceus</i>	R
Dcfl	Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>	R
Gcfl	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	M
Grki	Great Kiskadee	<i>Pitangus sulphuratus</i>	R
Bbfl	Boat-billed Flycatcher	<i>Megarhynchus pitangua</i>	R
Sofl	Social Flycatcher	<i>Myiozetetes similis</i>	R
Mati	Masked Tityra	<i>Tityra semifasciata</i>	R
Grja	Green Jay	<i>Cyanocorax yncas</i>	R
Brja	Brown Jay	<i>Cyanocorax morio</i>	R
Bcja	Bushy-crested Jay	<i>Cyanocorax melanocyanea</i>	R
Bbwr	Band-backed Wren	<i>Campylorhynchus zonatus</i>	R
Plwr	Plain Wren	<i>Thryothorus modestus</i>	R
Sbwr	Spot-breasted Wren	<i>Thryothorus maculipectus</i>	R
Wbwv	White-breasted Wood-wren	<i>Henicorbina leucosticta</i>	R
Bggn	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	M
Scso	Slate-colored Solitaire	<i>Myadestes unicolor</i>	R
Swth	Swainson's Thrush	<i>Catharus ustulatus</i>	M
Woth	Wood Thrush	<i>Hylocichla mustelina</i>	M
Blro	Black Robin	<i>Turdus infuscatus</i>	R
Ccro	Clay-colored Robin	<i>Turdus grayi</i>	R
Grca	Gray Catbird	<i>Dumetella carolinensis</i>	M
Cewa	Cedar Waxwing	<i>Bombocilla cedrorum</i>	M
Sovi	Solitary Vireo	<i>Vireo solitarius</i>	M
Legr	Lesser Greenlet	<i>Hylophilus decurtatus</i>	R
Tewa	Tennessee Warbler	<i>Vermivora peregrina</i>	M
Yewa	Yellow Warbler	<i>Dendroica petechia</i>	M
Cswa	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	M
Mawa	Magnolia Warbler	<i>Dendroica magnolia</i>	M
Btgw	Black-throated Green Warbler	<i>Dendroica virens</i>	M
Bwwa	Black-and-white Warbler	<i>Mniotilta varia</i>	M
Amre	American Redstart	<i>Setophaga ruticilla</i>	M
Oven	Ovenbird	<i>Seiurus aurocapillus</i>	M

Appendix A. Continued

Code	Common Name	Genus and Species	Status*
Kewa	Kentucky Warbler	<i>Oporornis formosus</i>	M
Mgwa	Macgillivray's Warbler	<i>Oporornis tolmiei</i>	M
Coye	Common Yellowthroat	<i>Geothlypis trichas</i>	M
Howa	Hooded Warbler	<i>Wilsonia citrina</i>	M
Wiwa	Wilson's Warbler	<i>Wilsonia pusilla</i>	M
Stre	Slate-throated Redstart	<i>Myioborus miniatus</i>	R
Gcrw	Golden-crowned Warbler	<i>Basileuterus culicivorus</i>	R
Rcwa	Rufous-capped Warbler	<i>Basileuterus rufifrons</i>	R
Ybch	Yellow-breasted Chat	<i>Icteria virens</i>	M
Gmta	Golden-masked Tanager	<i>Tangara larvata</i>	R
Grho	Green Honeycreeper	<i>Chlorophanes spiza</i>	R
Bcch	Blue-crowned Chlorophonia	<i>Chlorophonia occipitalis</i>	R
Yteu	Yellow-throated Euphonia	<i>Euphonia hirundinacea</i>	R
Bheu	Blue-hooded Euphonia	<i>Euphonia elegantissima</i>	R
Obeu	Olive-backed Euphonia	<i>Euphonia gouldi</i>	R
Ywta	Yellow-winged Tanager	<i>Thraupis abbas</i>	R
Rtat	Red-throated Ant-tanager	<i>Habia fuscicauda</i>	R
Suta	Summer Tanager	<i>Piranga rubra</i>	M
Weta	Western Tanager	<i>Piranga ludoviciana</i>	M
Fcta	Flame-colored Tanager	<i>Piranga bidentata</i>	R
Ccta	Crimson-collared Tanager	<i>Phlogothraupis sanguinolenta</i>	R
Cbta	Common Bush-tanager	<i>Chlorospingus ophthalmicus</i>	R
Btsa	Buff-throated Saltator	<i>Saltator maximus</i>	R
Bhsa	Black-headed Saltator	<i>Saltator atriceps</i>	R
Rbgr	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	M
Blgr	Blue Grosbeak	<i>Guiraca caerulea</i>	M
Inbu	Indigo Bunting	<i>Passerina cyanea</i>	M
Obsp	Orange-billed Sparrow	<i>Arremon aurantiostris</i>	R
Wfgs	White-faced Ground-sparrow	<i>Melospiza biarcuatum</i>	R
Bblg	Blue-black Grassquit	<i>Volatinia jacarina</i>	R
Wcse	White-collared Seedeater	<i>Sporophila torquella</i>	R
Yfgr	Yellow-faced Grassquit	<i>Tiaris olivacea</i>	R
Rusp	Rusty Sparrow	<i>Aimophila rufescens</i>	R
Mebl	Melodious Blackbird	<i>Dives dives</i>	R
Gtgr	Great-tailed Grackle	<i>Quiscalus mexicanus</i>	R
Oror	Orchard Oriole	<i>Icterus spurius</i>	M
Ybor	Yellow-backed Oriole	<i>Icterus chrysater</i>	R
Ytor	Yellow-tailed Oriole	<i>Icterus mesomelas</i>	R
Baor	Baltimore Oriole	<i>Icterus galbula</i>	M
Ybca	Yellow-billed Cacicque	<i>Amblycercus holosericeus</i>	R
Chor	Chestnut-headed Oropendola	<i>Oropendola wagleri</i>	R

*R = resident and M = migrant.