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. Of the coffee plantation habitats, Inga shade had the highest diversity. Species associated with wooded vegetation were more common in shade plantations, particularly in Inga. Bird numbers declined during the second census period and this decline 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 plantations previously studied in nearby Chiapas, México. The relatively low diversity was probably due to the low stature, tree species diversity, and heavy pruning of the canopy. These features reflect management practices that are common throughout Latin America. 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 the forest patch habitats. 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 will only be important for avian diversity if a tall, taxonomically and structurally diverse canopy is maintained. We suggest that this is most likely on farms that are managed for a variety of products rather than those oriented entirely towards production of coffee.

Introduction

As more land is converted from natural vegetation to farms and pasture, the role of different agroecosystems in conserving biological diversity is receiving more attention (Pimental et al. 1992). Agricultural systems that incorporate trees, which provide increased structural complexity and resources, are often considered to be 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 biodiversity. Ornithologists in particular often 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 and Waide 1993, Vannini 1994, Greenberg in review, Wunderle and Latta in review) and other aspects of biological diversity (Nestel et al. 1993, Perfecto and Vandermeer 1994, Perfecto et al. in review).

In the past two decades, much of what used to be shade coffee plantation has been converted into sun or "semi-shade" plantations, where most or all of the canopy trees are removed (Rice 1992). This cultivation system combined with increased inputs of agrochemicals is often able to produce much higher yields of coffee. Sun coffee plantations lack the canopy trees which 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 and Latta in review).

There is a danger in adopting a dichotomous sun versus shade classification in studying the impact of coffee cultivation. The shade canopy of coffee plantations is managed in a wide 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 a class. For example, in some coffee growing areas, 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 monoculture of short-stature shade trees (*Inga* spp., *Gliricidia sepium*, and *Erythrina* spp.). Trees are often trimmed twice each year to maintain their parasol architecture casting a monolayer of shade (Castillo 1994), and to avoid too much humidity which is thought to favor fungal disease.

Previously, Greenberg (in review) reported on the high diversity of birds associated with traditional mixed and rustic plantations in eastern Chiapas. In this paper 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 of primarily *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 altitudinal band as the coffee zone.

Study Sites

The study was conducted in foothills of the Sierra de las Minas in the Polochic Valley (Departamento de Alta Verapaz). Bird surveys were conducted in the following areas: Tamahú (15° 8'N, 90° 14'W), Tucurú (15° 8'N, 90° 7'W), Jolomjix (15° 16'N, 89° 45'W), and Pueblo Viejo (15° 18'N, 89° 41'W). The sites ranged from 102 to 1230 m in elevation (see habitat descriptions). 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/semi-shade (referred to as sun). The basic descriptive statistics can be found in Table 1. *Inga* shade grows at higher elevations than *Gliricidia*, whereas sun plantations can be found throughout the elevational gradient.

Both plantation types are 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. *Gliricidia* plantations are strongly dominated (85%) by the most common tree (vs 61% for *Inga*) and showed considerably lower vertical structural complexity compared to *Inga* plantations (SD of tree height = 0.7 versus 1.4 m, 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 *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). The 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 consider cardamom to be 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 as the 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). 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 during the period 06:45 - 10:00, 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. In this analysis we exclude individuals that were flying over the point. In addition, the surveyor recorded the elevation (based on altimeter readings), number of trees, the estimated canopy height as well as the aerial 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.

For species richness, we present the total number of species recorded on point counts for a habitat. In order to bring the large (204 points) Inga sample into line with the other habitats, we randomly selected 106 points. In order to control for different sampling effort, we conducted a rarefaction analysis (James and 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) which is *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 (Wilkenson 1990) using single-linkage nearest-neighbor method based on euclidean distance.

To examine variation in the abundance of total birds, residents, migrants, and common species (>0.10/pt for at least one habitat), we conducted a two-way ANOVA for habitat and between-period variation. We classified species based on whether they were found to be 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 includes species 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 Kruskall-Wallis test.

We examined features that correlated with the abundance of total birds, residents, and migrants by entering habitat variables into a multiple regression (SAS 1989). 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, standard deviation of height of trees (as an index of vertical complexity), shade cover, and coffee cover. First, all variables were entered into a step-wise multiple regression (forward selection). These variables were entered into a multiple regression model to obtain the Type II partial correlation coefficient to assess their relative contribution to the overall R^2.

Since in other regions we have found the flowering of Inga attracts large numbers of nectarivorous or omnivorous species, we conducted focal watches totalling 27 hrs at 9 different patches of flowering Inga edulis between 22 March and 1 April. In this paper 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

Total species richness cannot be compared statistically since only one number is derived from the total survey. However, 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). 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. However, the number of species recorded was lower in all habitats. This reduction was apparently not the result simply of migratory species leaving, since in every case the number of resident species declined as well (Table 2).

The number of migrant species was similar among habitats (23-29), with more variation found in resident species: Inga had 48, compared to 38 for Gliricidia and 40 for sun in Period 1, and 42, compared to 33 for sun and Gliricidia in period 2. Inga was similar to matorral (47 and 43 species in Period 1 and 2) and considerably lower than forest and cardamom (63 and 93, respectively).

When only regular species are considered (>.05 individuals/point, Table 3), coffee plantations had 21-27 species in period 1, compared to 36 species in matorral, 43 species in remnant, and 54 species in cardamom. This pattern is similar in period 2, with a disproportionate reduction in species in Gliricidia. Once again, most of the variation is found in the resident species totals.

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

Faunal Similarities

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

Bird Abundance

The abundance of migratory birds was generally similar between the three Polochic Valley coffee plantation habitats (Table 2). However, there was a marked difference in the degree to which migrants declined between periods, with Gliricidia losing 50 % of its individuals. A two-way ANOVA (habitat versus period) produced a significant period effect ($F_{1,852}$ = 10.05) and habitat X period interaction ($F_{2,852}$ = 3.2). Resident numbers differed significantly between habitats ($F_{2,852}$ = 12.8) with a significant habitat X period effect ($F_{2,852}$ = 3.3). Sun coffee had significantly fewer birds than the other habitats, based on a Bonferroni post-hoc comparison. Finally, total birds per point showed a significant habitat ($F_{2,852}$ = 8.7) and period effect ($F_{1,852}$ = 6.4), with Inga having significantly more birds than the other habitats, and the early season having more birds than the later.

Individual Species

Of the migratory species analyzed in a two-way ANOVA, we found all but one species were most common in one of the shade plantation types (Table 5). Woodland migrants tended to be most common in Inga, and shrub migrants were most common in Gliricidia.

All resident forest species were significantly more common in shade plantations, with four most common in Inga and two in Gliricidia. This pattern may be a result of the elevational difference between the two shade types, as great kiskadees and yellow-olive flycatchers are lowland species found most commonly in Gliricidia plantations. Resident scrub species are evenly split between preferring sun and shade plantations.

The proportion of migrants and residents showing a significant seasonal effect were similar (5/11 and 6/13, respectively). In most cases (9/11) birds were detected more on early rather than later surveys. The exceptions are the granivorous indigo bunting and white-faced ground sparrow and the nectarivorous azure-crowned hummingbird.

Forest and Scrub Birds in Coffee Plantations

There was significant between-plantation-type variation in the ranking of forest migrants (Kruskall-Wallis = 14.7, $P < .001$) during the early (but not late) season, with Gliricidia and Inga having more forest migrants than sun coffee (Table 6). The difference between habitats for scrub migrants was not significant. We also found significant variation between habitats in the ranking of forest residents: KW = 21.7, $P < .001$, for early, and KW = 19.0, $P < .001$, for late census. 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 was significantly related to the standard deviation of tree height, and to the number of tree species, and negatively related to elevation in period I (Table 7), and mean height and standard deviation of height in Period II. The model is highly significant but explains only a small proportion of the total variance (R^2 = 0.13 and .095, respectively). Resident birds show a similar pattern (R^2 = 0.13 for both periods) with a model based on a positive relation with standard deviation of tree height and tree species, and negatively related to elevation and tree dominance for period I, and positively related to mean height and tree species, and negatively related to tree dominance for the second period. The models for migrants are considerably weaker (R^2 = .038 and .029 for periods I and II, respectively). In this case the important variables are tree number, tree species, and (negatively) elevation for Period I. Period II deviates from this, with standard deviation of tree height the only variable accepted into the model. The multivariate models generally include the most highly correlated variables in univariate analyses. The major exception is shade cover, which is consistently one of the most highly correlated variable, but is dropped from all step-wise models because of its collinearity with other variables (i.e., tree height and number).

Use of Shade Trees Versus Coffee Bushes

Overall, birds were recorded in trees in coffee plantations far more often than in the coffee layer (74 % of total observations). Three of the 6 common migrants (those occurring with an abundance of > .10 in any habitat, Table 5) and 8/12 residents were specialized in occurring in canopy trees (> 80%), with only Wilson's warbler, yellow-faced grassquit, blue-black grassquit and rufous-capped warbler specialized on the coffee layer.

Use of Flowering _Inga_

We observed only seven species feeding on _Inga_ flowers during our focal observations (Table 9). Of these, over half were made by one species of hummingbird (azure-crowned) and over two-thirds were made by two species of hummingbird (adding rufous-tailed hummingbird). Other visitors were either hummingbirds or icterids. Interestingly, we did not record Tennessee warblers during these focal watches. Tennessee warblers feed commonly on _Inga_ but occur patchily in large flocks, and are easily missed on surveys like this.

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 as well. 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_. 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. Resident birds showed the strongest correlation with a multivariate model of habitat variables. In general, variables that relate to the vertical structure and taxonomic diversity of the canopy contributed the most to the model.

As in previous studies, the comparisons are necessarily confounded by elevation. This is most evident in the comparison between *Gliricidia* versus *Inga* sun plantations. *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/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 upper *Gliricidia* and *Inga* belts and so are probably comparable with the *Inga* plantations.

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 coffee plantations. It appears that diversity and density of all birds are substantially higher in matorral. 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 (in prep., reported for cattle pastures Greenberg and Salgado 1994). The coffee layer provides few resources for omnivorous or granivorous birds (which dominate matorral) since "weeds" are discouraged through the use of herbicides. Coffee 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), which includes heavily defended or "tough" leaves (Frischknecht et al. 1986) which may be one of the reasons they support a low density of herbivorous arthropods (unpubl. data). In a bird exclosure study conducted contemporaneously with this project, we found that arthropod biomass per 100 g leaf biomass was approximately 6 times greater for Inga than shade coffee foliage (.639 vs. .111) and over 14 times greater than sun coffee foliage (.043 g) (unpubl. data).

Comparison with 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 and Bichier in review). We observed approximately half the number of birds per point and only two-thirds the species richness in approximately 100 survey points. Furthermore, the Guatemalan plantations were almost completely devoid of even the most generalized forest resident species. Because rustic and Inga plantations had similar levels of diversity and bird abundance, 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.

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 similar numbers of birds per point and diversity to the coffee plantations of Ocsosingo, it is likely that the lower abundance and diversity of birds in the Guatemalan plantation relate 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 could support mosses, lichens and epiphytes, which in turn can support a number of birds missing from the Guatemalan plantations (woodcreepers, euphonias, etc.).

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 (Vannini 1994, Greenberg in review). The only species showing significant increases in Inga plantations at the time of flowering was the azure-crowned hummingbird. During focal observation of Inga, this was the dominant species foraging on flowers, commonly establishing feeding territories around a patch of flowering trees. Therefore, based on our observations of resource use, the restriction of a migratory influx to this one hummingbird species is not surprising. Once again, we believe that the extensive pruning, which reduces tree size and may affect flowering, may underlie the lack of nectarivores in the Polochic plantations.

Conclusions

1. 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 are less common or missing from sun plantations or those where the shade is dominated by the deciduous Gliricidia trees.

2. The number of birds per point, particularly resident birds, is generally related to variables that describe the height and structural diversity of the canopy.

3. Based on comparisons with more forest-like and traditional plantations in Chiapas, Mexico, we conclude that the heavy shade management of the Polochic plantations reduces the resources for a substantial number of forest species.

4. 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 in 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 input necessary for the continued cultivation of sun coffee and there is a de facto regeneration of shade trees. This apparently occurred during the most recent depression in coffee prices from 1989-1994 (Perfecto pers. comm.). 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 (Arjona 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 presence of shade is only part of the story. The benefits of coffee cultivation to the conservation of biodiversity will only be fully realized adhering 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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Table 1. Descriptive statistics for habitats surveyed based on estimates made at point count circles. (Mean, SD, and range). Measurements are in meters.

Habitat	N	Elevation ft (m)	Canopy Cover (%) Period I	II	Tree Species	Tree/ha	X Tree Height	SD Tree Height	Tree Dominance#	Coffee Cover (%)
Inga	204	786 (197) 369-1185*	50 (18)	39 (19)	3.8 (1.7)	153 (71)	6.9 (1.4)	1.38 (1.15)	0.60 (.06)	66 (20)
Gliricidia	102	447 (99) 102-692*	35 (14)	40 (15)	3.7 (2.2)	245 (82)	6.7 (1.0)	0.77 (.66)	0.83 (.17)	65 (25)
Sun/Semi-shade	104	646 (243) 262-1231*	7 (7)	5 (7)	2.8 (1.5)	66 (33)	4.7 (1.4)	0.74 (1.05)	0.55 (.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)		

* Elevation Range

Tree Dominance: *Inga* or *Gliricidia* / total trees

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)
Inga (108,106)	73	62.1 (3.2)	65	55.5 (3.1)
Gliricidia (103,102)	64	58.1 (2.0)	53	46.3 (0.8)
Sun (110,133)	65	58.7 (1.6)	55	49.2 (1.2)
Matorral (77,56)	70	64.3 (2.0)	63	61.2 (1.24)
Forest Remnant (71)			87	72.2 (2.3)
Cardamom (101)	122			

Table 3. Total number of species, total species (0.05 ind. per point), and average number of individual migrant and resident species per point.

Habitat	Period I Migrant	Period I Resident	Period II Migrant	Period II Resident
Inga	29, 9, 2.5	48, 13, 3.1	23, 6, 2.0	42, 12, 3.2
Gliricidia	25, 13, 3.2	38, 14, 2.4	20, 6, 1.6	33, 13, 2.6
Sun	26, 9, 2.0	40, 12, 2.4	22, 8, 1.9	33, 10, 1.5
Matorral	23, 13, 3.3	47, 23, 3.9	20, 12, 3.0	43, 22, 4.8
Forest Remnant			23, 9, 2.9	63, 34, 5.8
Cardamom	29, 16, 4.4	93, 38, 4.9		

Table 4. Mean number of individuals per point of birds (minimum 0.05 ind./point) on point counts in the seven major habitats studied. Values are for Period I and II, respectively. See Appendix A for full English name and Latin name of all species included in this table (S scrub, F forest --see methods).

	Inga	Gliricidia	Sun	Scrub	Cardamom	Remnant
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

Inga	Gliricidia	Sun	Scrub	Cardamom	Remnant
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 0.00	Brja 0.11 0.00	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	Rbaz 0.05 0.06	Wcpa 0.05 0.00	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 0.00 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 0.00S	Yteu 0.08F	Stre 0.11F
	Rbpi 0.00 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	Btsa 0.07
			Rbaz 0.03 0.09	Coar 0.07F	Yofl 0.07
			Dcfl 0.03 0.09	Fcta 0.07F	Cotr 0.07F

Table 5. Results of two-way ANOVA for the effects of habitat and season on the abundance of common birds in coffee plantations in the Polochic Valley.

Habitat	Season	Habitat X Season

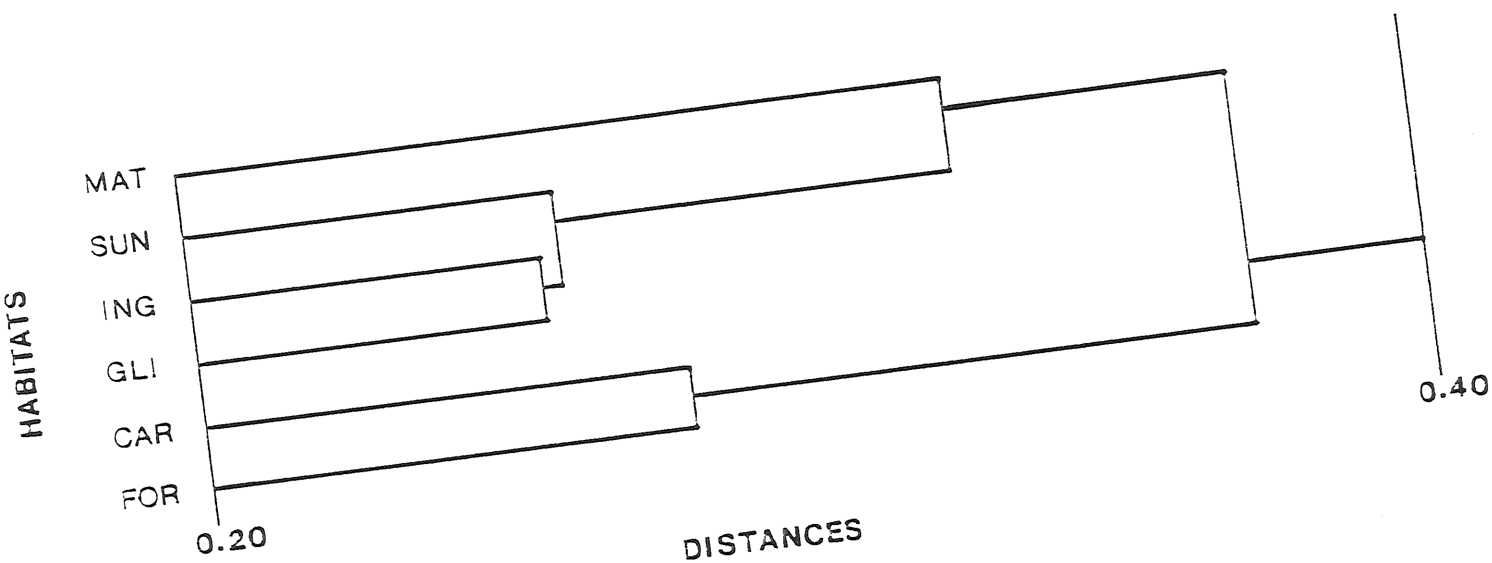
Residents	Inga	Gliricidia	Sun	Scrub	Cardamom	Remnant
				Brja 0.03 0.07	Rthu 0.07	Bcmo 0.07
				Chor 0.01 0.13	Ywta 0.07F	Obsp 0.07
				Btsa 0.00 0.05	Mebl 0.07	Ccro 0.07
					Rcwa 0.06	Yteu 0.07
					Emto 0.06F	Blro 0.07
					Ybor 0.06	Dcfl 0.06
					Bcmo 0.06F	Visa 0.06
					Gmta 0.05F	Brat 0.06
					Ccwo 0.05F	Erfl 0.06
					Scfl 0.05F	
					Scso 0.05F	
					Sbwr 0.05	
					Kbto 0.05F	
					Obfl 0.05F	

	F-Value	P	Pair-wise Difference	F-Value	P	Difference	F-Value	P
<u>Forest Migrant Species</u>								
Yellow-bellied flycatcher	2.50	.083		0.013	.910		0.026	.975
Blue-gray gnatcatcher	8.42	.000	<u>Gliricidia</u> > sun / <u>Inga</u>	15.78	.000		8.42	.000
Wood thrush	5.50	.004	<u>Inga</u> > sun / <u>Gliricidia</u>	4.87	.028	early > late	3.88	.021
Tennessee warbler	6.19	.002	<u>Inga</u> > sun	0.05	.824		0.28	.755
Black-throated green warbler	16.65	.000	<u>Inga</u> > sun / <u>Gliricidia</u>	8.17	.004	early > late	2.87	.060
<u>Shrub Migrant Species</u>								
Ruby-throated hummingbird	15.18	.000	<u>Gliricidia</u> / sun > <u>Inga</u>	0.35	.557		14.41	.000
Magnolia warbler	28.79	.000	<u>Gliricidia</u> > sun > <u>Inga</u>	3.86	.050	early > late	0.47	.626
Yellow warbler	13.00	.000	<u>Gliricidia</u> > sun / <u>Inga</u>	0.01	.936		1.24	.291
Least flycatcher	30.76	.001	<u>Gliricidia</u> > sun > <u>Inga</u>	17.71	.001	early > late	4.43	.012
Wilson's warbler	0.25	.776		0.77	.380		0.75	.474
Indigo bunting	18.87	.000	sun / <u>Inga</u> > <u>Gliricidia</u>	6.98	.008	late > early	5.84	.003
<u>Forest Resident</u>								
Golden-fronted woodpecker	16.41	.000	<u>Inga</u> > <u>Gliricidia</u> / sun	0.38	.540		1.14	.321
Azure-crowned hummingbird	16.17	.000	<u>Inga</u> > <u>Gliricidia</u> > sun	8.13	.004	late > early	5.56	.006
Great kiskadee	4.27	.014	<u>Gliricidia</u> > sun / <u>Inga</u>	6.62	.010	early > late	2.56	.078
Yellow-olive flycatcher	14.77	.000	<u>Gliricidia</u> > sun / <u>Inga</u>	3.34	.037	early > late	0.608	.544
Clay-colored robin	5.50	.011	<u>Inga</u> > <u>Gliricidia</u> / sun	4.45	.035	early > late	1.27	.283
Chestnut-headed oropendola	3.53	.046	<u>Inga</u> > sun	7.24	.012	early > late	0.84	.433
Black-headed saltator	2.47	.085		0.59	.445		1.19	.304
<u>Scrub Resident</u>								
Rufous-tailed hummingbird	1.54	.216		0.65	.419		2.56	.078

Groove-billed ani	5.74	.003	<u>Gliricidia</u> > sun / <u>Inga</u>	0.91	.342		0.72	.487
Brown jay	3.09	.046	<u>Inga</u> > sun	0.07	.622		2.24	.107
Rufous-capped warbler	3.60	.008	<u>Inga</u> / sun > <u>Gliricidia</u>	1.14	.286		1.61	.200
Yellow-faced grassquit	33.84	.000	sun > <u>Gliricidia</u> / <u>Inga</u>	7.88	.005	early > late	6.84	.001
White-faced ground sparrow	11.36	.000	sun > <u>Gliricidia</u> / <u>Inga</u>	4.16	.042	late > early	2.76	.064
Melodious blackbird	20.24	.000	<u>Inga</u> > <u>Gliricidia</u> / sun	1.54	.215		0.317	.728
Great-tailed grackle	1.52	.220		0.55	.459		1.50	.224

Table 6. Mean ranking of abundance for forest versus scrub migrants and residents in the two census periods for the Polochic Valley coffee plantations.

	Inga		*Gliricidia*		Sun	
	Period I	II	Period I	II	Period I	II
Forest Migrants (N = 10,11 spp.)	1.6 (0.7)	1.6 (0.7)	1.6 (0.5)	2.2 (0.7)	2.8 (0.6)	2.1 (0.9)
Forest Residents (N=19,13 spp.)	1.4 (0.7)	1.3 (0.5)	2.1 (0.6)	2.0 (0.8)	2.6 (0.5)	2.7 (0.4)
Scrub Migrants (N=8,5 spp.)	2.2 (0.8)	1.8 (0.8)	2.1 (0.9)	2.7 (0.1)	1.7 (0.6)	1.5 (0.4)
Scrub Residents (N=17,16 spp.)	2.1 (0.7)	2.2 (0.7)	2.2 (0.9)	1.9 (0.8)	1.9 (0.7)	1.9 (0.9)


MAT
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DISTANCES
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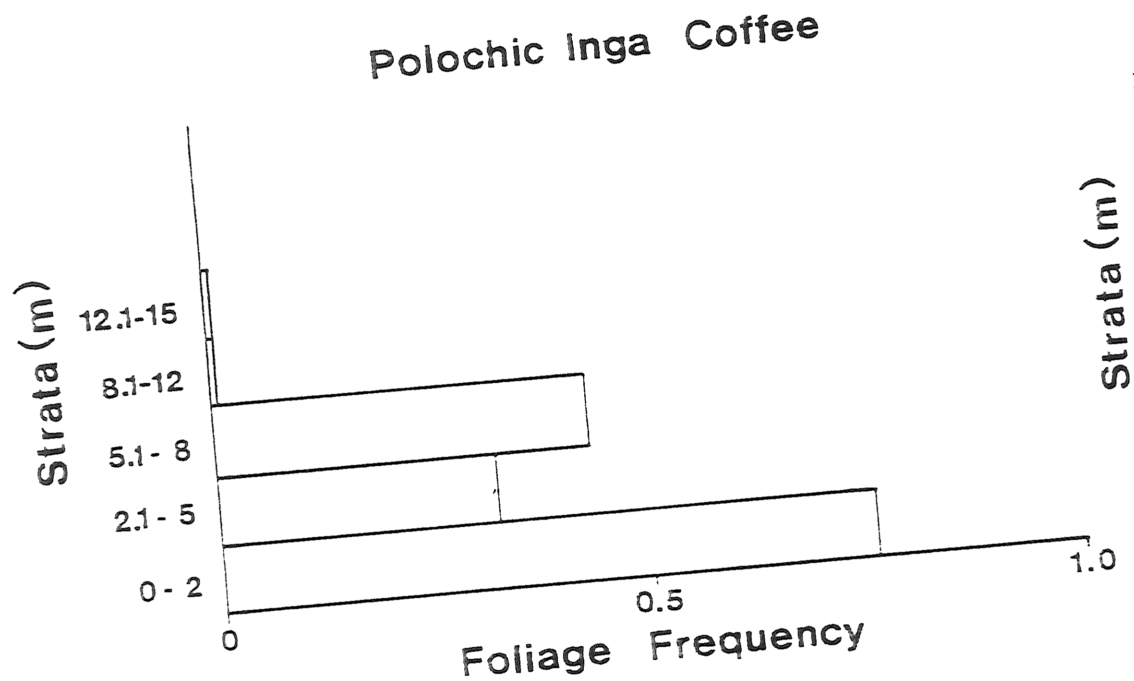
Polochic Inga Coffee
Strata (m)
12.1-15
8.1-12
5.1- 8
2.1- 5
0 - 2
0
0.5
1.0
Foliage Frequency

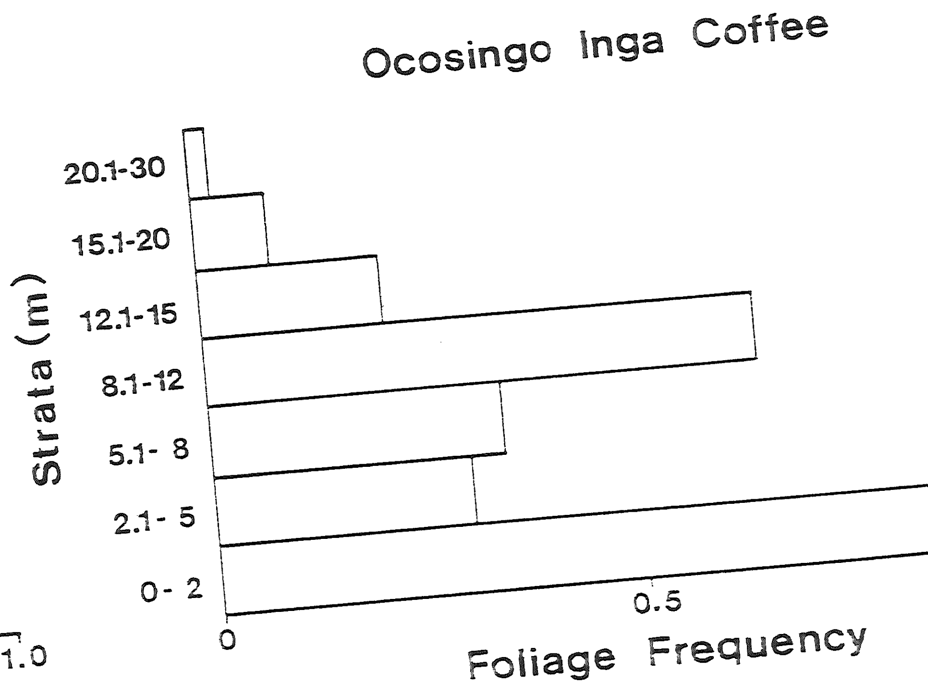
Ocosingo Inga Coffee
Strata (m)
20.1-30
15.1-20
12.1-15
8.1-12
5.1- 8
2.1- 5
0- 2
0
0.5
Foliage Frequency

Table 7. Summary statistics for regression of total birds, residents, and migrants per point versus habitat variables (see Methods). Variables were selected using forward stepwise multiple regression and Type II partial correlations calculated to indicate the importance of each variable to the overall model.

Habitat Status	Period I R^2	Period I Variable	Period I Partial r^2	Period II R^2	Period II Variable	Period II Partial r^2
Total	.129	Elevation	-.034	.095	SD Tree Height	.040
		Tree Species	.033		X Tree Height	.023
		SD Tree Height	.030			
Resident	.132	SD Tree Height	.036	.131	X Tree Height	.057
		Elevation	-.025		Tree species	.020
		Tree Species	.013		Tree Dominance	-.018
		Tree Dominance	-.007			
Migrants	.038	Tree Species	.012	.029	SD Tree Height	.029
		Elevation	-.011			
		Tree Number	.008			

Table 8. Percentage use of shade trees versus by common species in coffee plantations.

Species	Period I	Period II
Least flycatcher	69 (42)	44 (20)
Blue-gray gnatcatcher	100 (11)	
Tennessee warbler	88 (64)	81 (59)
Yellow warbler	94 (32)	94 (35)
Magnolia warbler	54 (99)	45 (84)
Black-throated green warbler	92 (188)	83 (128)
Wilson's warbler	27 (93)	30 (71)
Total Migrants	70 (672)	64 (478)
Groove-billed ani	67 (3)	84 (6)
Yellow-olive flycatcher	100 (8)	100 (4)
Greater kiskadee	100 (10)	100 (4)
Clay-colored robin	94 (32)	88 (67)
White-faced ground sparrow	33 (3)	0 (9)
Yellow-faced grassquit	8 (13)	0 (11)
Melodious blackbird	97 (59)	97 (103)
Great-tailed grackle	86 (7)	91 (11)
Chestnut-headed oropendola	100 (43)	100 (33)
Rufous-capped warbler	6 (35)	22 (49)
Blue-black grassquit	0 (9)	0 (7)
Black-headed saltator	86 (29)	100 (30)
Total Residents	79 (495)	83 (648)

Table 9. The number and percentage of visits to *Inga* flowers during 27 hours of focal observation at 9 different *Inga* patches during peak flowering.

Species	Total	Percentage
Azure-crowned hummingbird	47	49.5
Rufous-tailed hummingbird	21	22.1
Yellow-tailed oriole	7	7.4
Spot-breasted oriole	7	7.4
Chestnut-headed oropendola	4	4.2
Fork-tailed emerald	4	4.2
Melodious blackbird	3	3.1
Long-tailed hermit	1	1.1
Green-breasted mango	1	1.1
Total	95	

Figure Captions

Figure 1. Cluster analysis, based on Dice's Similarity Index, of habitats surveyed in the Polochic Valley, Guatemala. Habitat acronyms are: Mat = Mattoral, Sun = Sun/semishade coffee, Ing = Inga Coffee, Gli - Gliricidia Coffee, Car = Shade cardamon, For = Forest remnant.

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.

Appendix A. Species Code, English, and Latin species names, and migratory status (R = resident, M = migrant).

	Code	English Name	Latin Name	Status
1	Plch	Plain chachalaca	Ortalis vetula	R
2	Rbpi	Red-billed pigeon	Columba flavirostris	R
3	Wtdo	White-tipped dove	Leptotila verreauxi	R
4	Otpa	Olive-throated parakeet	Aratinga astec	R
5	Wcpa	White-crowned parrot	Pionus senilis	R
6	Gban	Groove-billed ani	Crotophaga sulcirostris	R
7	Lihe	Little hermit	Phaethornis longuemareus	R
8	Visa	Violet sabrewing	Campylopterus hemileucurus	R
9	Ftem	Fork-tailed emerald	Chlorostilbon canivettii	R
10	Rthu	Rufous-tailed hummingbird	Amazilia tzacatl	R
11	Rbaz	Red-billed azurecrown	Amazilia cyanocephala	R
12	Ruth	Ruby-throated hummingbird	Archilochus colubris	M
13	Cotr	Collared trogon	Trogon collaris	R
14	Bcmo	Blue-crowned motmot	Momotus momota	R
15	Emto	Emerald toucanet	Aulacorhynchus prasinus	R
16	Coar	Collared aracari	Pteroglossus torquatus	R
17	Kbto	Keel-billed toucan	Ramphastos sulfuratus	R
18	Gfwo	Golden-fronted woodpecker	Melanerpes aurifrons	R
19	Gowo	Golden-olive woodpecker	Piculus rubiginosus	R
20	Ccwo	Chestnut-colored woodpecker	Celeus castaneus	R
21	Shwo	Streak-headed woodcreeper	Lepidocolaptes souleyetii	R
22	Baan	Barred antshrike	Thamnophilus doliatus	R
23	Obfl	Ochre-bellied flycatcher	Mionectes oleagineus	R
24	Scfl	Sepia-capped flycatcher	Leptopogon amaurocephalus	R
25	Erfl	Eye-ringed flatbill	Rhynchocyclus brevirostris	R
26	Yofl	Yellow-olive flycatcher	Tolmomyias sulphurescens	R
27	Ybfl	Yellow-bellied flycatcher	Empidonax flaviventris	M
28	Lefl	Least flycatcher	Empidonax minimus	M

29	Brat	Bright-rumped attila	Attila spadiceus	R
30	Dcfl	Dusky-capped flycatcher	Myiarchus tuberculifer	R
31	Gcfl	Great-crested flycatcher	Myiarchus crinitus	M
32	Grki	Great kiskadee	Pitangus sulphuratus	R
33	Bbfl	Boat-billed flycatcher	Megarhynchus pitangua	R
34	Sofl	Social flycatcher	Myiozetetes similis	R
35	Mati	Masked tityra	Tityra semifasciata	R
36	Grja	Green jay	Cyanocorax yncas	R
37	Brja	Brown jay	Cyanocorax morio	R
38	Bcja	Bushy-crested jay	Cyanocorax melanocyanea	R
39	Bbwr	Band-backed wren	Campylorhynchus zonatus	R
40	Plwr	Plain wren	Thryothorus modestus	R
41	Sbwr	Spot-breasted wren	Thryothorus maculipectus	R
42	Wbww	White-breasted wood-wren	Henicorhina leucosticta	R
43	Bggn	Blue-gray gnatcatcher	Polioptila caerulea	M
44	Scso	Slate-colored solitaire	Myadestes unicolor	R
45	Swth	Swainson's thrush	Catharus ustulatus	M
46	Woth	Wood thrush	Hylocichla mustelina	M
47	Blro	Black robin	Turdus infuscaturs	R
48	Ccro	Clay-colored robin	Turdus grayi	R
49	Grca	Gray catbird	Dumetella carolinensis	M
50	Cewa	Cedar waxwing	Bombycilla cedrorum	M
51	Sovi	Solitary vireo	Vireo solitarius	M
52	Legr	Lesser greenlet	Hylophilus decurtatus	R
53	Tewa	Tennessee warbler	Vermivora peregrina	M
54	Yewa	Yellow warbler	Dendroica petechia	M
55	Cswa	Chestnut-sided warbler	Dendroica pensylvanica	M
56	Mawa	Magnolia warbler	Dendroica magnolia	M
57	Btgw	Black-throated green warbler	Dendroica virens	M
58	Bwwa	Black-and-white warbler	Mniotilta varia	M
59	Amre	American redstart	Setophaga ruticilla	M
60	Oven	Ovenbird	Seiurus aurocapillus	M

61	Kewa	Kentucky warbler	Oporornis formosus	M
62	Mgwa	Macgillivray's warbler	Oporornis tolmiei	M
63	Coye	Common yellowthroat	Geothlypis trichas	M
64	Howa	Hooded warbler	Wilsonia citrina	M
65	Wiwa	Wilson's warbler	Wilsonia pusilla	M
66	Stre	Slate-throated redstart	Myioborus miniatus	R
67	Gcrw	Golden-crowned warbler	Basileuterus culicivorus	R
68	Rcwa	Rufous-capped warbler	Basileuterus rufifrons	R
69	Ybch	Yellow-breasted chat	Icteria virens	M
70	Gmta	Golden-masked tanager	Tangara larvata	R
71	Grho	Green honeycreeper	Chlorophanes spiza	R
72	Bcch	Blue-crowned chlorophonia	Chlorophonia occipitalis	R
73	Yteu	Yellow-throated euphonia	Euphonia hirundinacea	R
74	Bheu	Blue-hooded euphonia	Euphonia elegantissima	R
75	Obeu	Olive-backed euphonia	Euphonia gouldi	R
76	Ywta	Yellow-winged tanager	Thraupis abbas	R
77	Rtat	Red-throated ant-tanager	Habia fuscicauda	R
78	Suta	Summer tanager	Piranga rubra	M
79	Weta	Western tanager	Piranga ludoviciana	M
80	Fcta	Flame-colored tanager	Piranga bidentata	R
81	Ccta	Crimson-collared tanager	Phlogothraupis sanguinolenta	R
82	Cbta	Common bush-tanager	Chlorospingus ophthalmicus	R
83	Btsa	Buff-throated saltator	Saltator maximus	R
84	Bhsa	Black-headed saltator	Saltator atriceps	R
85	Rbgr	Rose-breasted grosbeak	Pheucticus ludovicianus	M
86	Blgr	Blue grosbeak	Guiraca caerulea	M
87	Inbu	Indigo bunting	Passerina cyanea	M
88	Obsp	Orange-billed sparrow	Arremon aurantiirostris	R
89	Wfgs	White-faced ground-sparrow	Melozone biarcuatum	R
90	Bblg	Blue-black grassquit	Volatinia jacarina	R
91	Wcse	White-collared seedeater	Sporophila torqueola	R
92	Yfgr	Yellow-faced grassquit	Tiaris olivacea	R

93	Rusp	Rusty sparrow	Aimophila rufescens	R
94	Mebl	Melodious blackbird	Dives dives	R
95	Gtgr	Great-tailed grackle	Quiscalus mexicanus	R
96	Oror	Orchard oriole	Icterus spurius	M
97	Ybor	Yellow-backed oriole	Icterus chrysater	R
98	Ytor	Yellow-tailed oriole	Icterus mesomelas	R
99	Baor	Baltimore oriole	Icterus galbula	M
100	Ybca	Yellow-billed cacique	Amblycercus holosericeus	R
101	Chor	Chestnut-headed oropendola	Oropendola wagleri	R