

Avian Foraging Behavior in Two Different Types of Coffee Agroecosystem in Chiapas, Mexico

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ABSTRACT

This study describes the foraging ecology of birds during summer and winter in two different types of coffee agroecosystems in Chiapas, Mexico. Avian foraging behavior is documented in two agroecosystems of differing management intensity, structurally similar but with different levels of floristic diversity, during summer and winter seasons. The distribution of tree species used by birds was more even, and birds used a greater diversity of tree species, in the more diverse coffee shade system. Much of the variation in resource use derived from shifts in the use of flowers and fruit, highlighting the importance in resource phenology for birds. Insectivory was more frequent in winter than summer for the coffee layer, and in summer for the shade layer. Given the vegetative structural similarity of the two coffee agroecosystems included in this study, floristic differences probably accounted for much of the difference in the bird communities between the management systems, especially given the strong seasonal response to flowering and fruiting. This work suggests that plentiful and diverse food resources associated with the high diversity of plant species may facilitate coexistence of the high number of bird species found in shade-grown coffee agroecosystems.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: floristic diversity; frugivory; insectivory; nectivory; Neotropics; seasonal variation; tropical agriculture.

COFFEE AGRICULTURE IS RECOGNIZED FOR ITS POTENTIAL TO CONTRIBUTE TO BIODIVERSITY CONSERVATION in less-intensive farms, often referred to as shade grown (Perfecto *et al.* 1996). There is generally a higher abundance and diversity of birds in coffee agroecosystems using less-intensive management practices, especially the maintenance of a diverse shade canopy (Wunderle & Latta 1996; Greenberg *et al.* 1997a,b; Calvo & Blake 1998; Dietsch 2003). The recognition that structural and floristic diversity are correlated with avian diversity motivated initial efforts to identify and certify coffee agroecosystems that have conservation value (R. Greenberg, pers. comm.). However, the specific mechanisms behind this relationship are not well understood. An improved understanding of the foraging ecology of birds in coffee agroecosystems may improve conservation efforts and contribute to our understanding of the ecological relationships of birds in managed and unmanaged tropical ecosystems.

Previous studies have demonstrated the importance of the shade layer to foraging birds (Wunderle & Latta 1998). In particular, *Inga* spp. have been identified as providing important resources for insectivorous and nectivorous birds (Wunderle & Latta 1996, Greenberg *et al.* 1997a, Johnson 2000). Several studies have pointed at a paucity of resources in the coffee layer as limiting understory forest-associated birds in coffee agroecosystems (Greenberg *et al.* 1997a,b; Wunderle & Latta 1998; Wunderle 1999). In general, the hypothesis that increasing floristic diversity in the coffee shade canopy contributes to bird diversity and abundance by providing additional foraging opportunities is untested. Wunderle and Latta

(1998) demonstrated that the presence of shade trees, especially *Inga vera*, was a key determinant in predicting the presence of many birds species in the Dominican Republic. However, foraging behavior in coffee management systems with greater shade-tree diversity needs further exploration. Enhanced shade-tree diversity is one of the key criteria for programs that use shade-grown coffee certification as a conservation tool in managed tropical landscapes. Additional research on foraging behavior in coffee shade management systems with greater tree diversity can provide insights into the hypothesis that reductions in floristic diversity as coffee management practices were intensified led to avifaunal declines (Vannini 1994).

In addition, research is lacking on the seasonality of resource use. Greenberg *et al.* (1997b) found that shade coffee may be an important dry season refuge due to an influx of migrants and residents as the dry season progresses. Documenting resource use by birds during the dry season can help identify important tree species to target for farmer outreach by conservation programs working in managed landscapes. Also, from the farmer perspective the overall impact of birds on arthropods is of interest, particularly in the coffee layer. Birds may play a role in reducing pest outbreaks and overall herbivory that may affect crop productivity (Greenberg *et al.* 2000).

The objective of this study is to describe the foraging ecology of birds in two different types of coffee agroecosystems during summer and winter in Chiapas, Mexico. This aggregate examination of the entire avian community concentrates on variation in foraging behavior between two management systems and across seasons. In particular, we examine how avian use of habitat and food resources changes in response to increased vegetative and floristic diversity. Seasonal differences in aggregate foraging behavior that may result from the addition of large numbers of long-distance migratory birds are evaluated.

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METHODS

STUDY AREA.—This study was conducted in the Sierra Madre de Chiapas mountain range east of Tapachula, just north of the Guatemala border near the Pacific coast of the Soconusco region of Chiapas, Mexico, a major coffee-growing region with coffee grown at altitudes from 300 m to 1500 m. Within this mountain range, mist netting and foraging observations were conducted at 1000 m in two coffee agroecosystems of Finca Irlanda, a certified organic farm located at 15° 10' N, 92° 20' W. Both coffee agroecosystems use diverse shade with several *Inga* species (hereafter grouped together as *Inga*), *Alchornea latifolia* (referred to as *Alchornea*) and *Trema micrantha* (referred to as *Trema*) the most abundant trees in the shade canopy (Martinez & Peters 1996). However, one agroecosystem is managed to maintain a higher diversity and abundance of shade trees using additional planted native forest trees. This system is referred to in this study as Restoration because this approach could serve as a model to restore shade canopy tree diversity. Restoration has sufficient canopy cover, species richness, and abundance of shade trees to qualify as certified shade-grown coffee (Smithsonian Bird Friendly® Certification) but had not yet attained canopy height or structural diversity requirements at the time of this study (Mas & Dietsch 2004). The unaugmented normal production system (referred to as Production) used on the majority of acreage in Finca Irlanda is similar to other organic production systems in this region. Finca Irlanda is 300 ha in size with approximately 290 ha in coffee production, of which 40 ha is the Restoration management system. While differing in management intensity, both these agroecosystems are certified organic and would be classified as commercial polyculture (Moguel & Toledo 1999).

FORAGING BEHAVIOR.—Foraging observations were conducted in the two shade management systems: Production and Restoration. During summer (June–July 2000) and winter (January–February 2001), two plots of 5 ha each were established in each coffee management system. On successive days, observers were rotated through each plot in both management systems to equalize effort. Observers made slow patrols visiting all areas of the entire plot and noted foraging behavior of birds using a protocol adapted from Greenberg *et al.* (1999), based on Remsen and Robinson (1990). Birds were located visually and audibly to reduce bias toward conspicuous individuals or species. Observers collected data on as many individuals as possible, though in large mixed species flocks only a few individuals were observed for each species to prevent double counting. As part of this study, prior to conducting foraging observations, birds in each study plot were banded during 3 d of intensive mist netting with equal effort per plot. Band combinations were also noted to identify birds previously observed. For each foraging maneuver observed, height of the bird, plant height, canopy height, and foraging layer were noted (Ground, Herbaceous, Coffee, or Shade). The ground layer included soil, leaf litter, and woody debris lying on the ground. Herbaceous included all low-lying vegetation below the coffee layer. All noncoffee plants at or above the coffee layer were included in the shade layer. Generally, data for only one maneuver were collected for each bird, though for rare species and species of interest up to five maneuvers were recorded. The following characteristics of each

foraging maneuver were recorded: substrate of the prey item, initial and secondary maneuvers, attack mode, and identity of prey item (prey type). To reduce the number of categories for analysis, plant species where the birds was observed, substrate of the prey item, and prey type were grouped into simplified categories based on similarity of the original observations (*e.g.*, all arthropods were grouped together as a single prey type, and leaf top, leaf bottom, and live leaf curl were all grouped together as leaf).

VEGETATION SAMPLING.—In order to assess habitat available for foraging, eight vegetation plots for each management system were located at random within the study plots. The vegetation protocol used in this study was modified from the Breeding Biology Research and Monitoring Database (BBIRD) protocol for use in coffee agroecosystems (Martin & Geupel 1993, Mas & Dietsch 2003). Each vegetation sampling plot was established as a circle of 12 m radius within which all trees greater than 8.13 cm diameter at breast height (DBH) were identified to species when possible or to morpho-species. Height and DBH were recorded for each tree. Within a 5-m radius circle, the same data were collected for understory trees with a DBH of 2.54–8.13 cm. Since this study focused on coffee management systems, all coffee bushes were counted and heights measured within the 5 m radius.

Canopy cover was measured using a vertical densitometer (Stumpf 1993). Canopy sampling points were established at 4 m intervals along the north–south and east–west axes dividing the sampling circle into quadrants. In addition, two points in the middle of each quadrant were sampled for a total of 20 points. At each point, the vertical densitometer was used to determine if there was canopy vegetation directly overhead. Coffee was moved aside if necessary. The tree species of the vegetation cover was also noted. When there were multiple layers of vegetation from different species, only the highest vegetation was recorded. Additionally, at each axis point, leaf litter thickness and height of herbaceous vegetation were measured. Percentage of herbaceous cover was estimated for the 5 m radius circle.

STATISTICAL ANALYSIS.—Location generally does not change during a foraging bout, so only the first observation was used for the analysis of location-related variables. Foraging maneuvers and prey items change frequently within foraging bouts; consequently, the analysis of these variables used all observations up to the maximum of five consecutive maneuvers (Greenberg *et al.* 1999). Categorical variables were compared using contingency table χ^2 -tests, using the number of observations per category for each group (*i.e.*, seasons, management system, migratory status, *etc.*). For multivariate analyses of categorical variables, multiple logistic regression was used. For some categorical variables, if there were inadequate number of observations for analysis, categories were grouped by similarity. Infrequent and unusual categories were grouped into a catch-all category, Other. Infrequently used or unidentified tree species were grouped together as Other Trees.

Identification of arthropod prey to finer taxonomic rank, such as order or family, was generally difficult due to problems observing key characters in the field and poor arthropod taxonomic knowledge of observers. However, observers readily identified lepidopteran

prey due to conspicuous morphology of adults (wing shape) and larvae (caterpillars). To evaluate patterns of insectivory, goodness-of-fit tests were used to test whether arthropods were taken more frequently between seasons and management systems using a 50 percent predicted even distribution. Similarly, goodness-of-fit tests were used to evaluate tree species use for foraging in relation to shade tree availability. Available foraging tree distributions were calculated from basal area and canopy coverage proportions found in the randomly located vegetation sampling plots. StatView (v5.0.1, SAS Institute, Inc.) and SPSS (v10 for Macintosh, SPSS Inc.) were used for computer statistical analyses. Stata (Intercooled v8.2 for Macintosh, Stata Corp.) was used for multinomial logistic regression (mlogit).

The aggregate analysis presented here may mask some interesting patterns at the species level. Pooling species does, however, allow us to evaluate overall ecological impacts from birds that forage in coffee agriculture. Species level analysis may help explain some of the patterns observed in this study, although focusing on those species with adequate sample sizes for foraging behavior analysis neglects the ecological contributions from the sizeable portion of tropical bird communities represented by rare or low abundance species. A further evaluation of these data by species will provide insights into resource limitations faced by individual species and the factors that facilitate species coexistence in human-altered ecosystems (Dietsch 2003).

RESULTS

FORAGING OBSERVATIONS.—In total, 2220 foraging observations from 88 species were recorded (Table S1). During summer 2000, there were 1012 foraging observations from 55 breeding species. In winter 2001, with long distance Neotropical migratory species present, there were 1208 observations from 74 species (27 migrants). More species were observed in Restoration (1215 observations of 80 species) than in Production (994 observations of 59 species). The total percentage of birds banded is unknown, but 18.9 percent of foraging observation was from banded birds. The proportion of banded birds was lowest in winter because migrants were not banded (ranging from a low of 14.6% in the winter Production plot to 24.4% in summer Production). In winter, 44.9 percent of residents were banded.

VEGETATION.—Vegetation differed significantly between management systems in ground cover, canopy cover, overstory species richness, basal area, number of coffee bushes, and coffee height (Table 1). There was no difference in structural depth or in the vertical structural profile of the shade canopy (Dietsch 2003). The management systems differed significantly in shade tree composition with relative availability of shade-tree categories calculated using basal area and canopy cover (Table 2, $P < 0.0001$).

FORAGING PLANT SELECTION (USE VS. AVAILABILITY).—In the shade layer with all bird species pooled, birds used a different distribu-

TABLE 1. Characteristics of a production and a restoration coffee management system in Chiapas, Mexico. Average values are shown and asterisk indicates $P \leq 0.05$. N refers to number of variable radius vegetation plots in each management system.

| | Production (N = 9) | Restoration (N = 8) |
|--|--------------------|---------------------|
| Ground cover (%)* | 73.4 | 55.8 |
| Canopy cover (%)* | 44.4 | 75.6 |
| Overstory species richness ^{a*} | 3.0 | 5.1 |
| Overstory basal area (m ²)* | 60.2 | 97.3 |
| Overstory stems* | 7.0 | 10.3 |
| Overstory tree height (m) | 11.8 | 12.4 |
| Structural depth ^b (m) | 13.2 | 22.6 |
| Coffee bushes* | 30.6 | 18.6 |
| Coffee height (m)* | 1.8 | 2.5 |
| Slope* | 17.8 | 38.8 |
| Aspect | 177.3 | 144.3 |

^aPer 12-m radius vegetation sampling plot (0.045 ha).

^bFrom Mas and Dietsch 2003.

tion of plants species than the actual distribution of plants available in both management systems (Table 2). In Production, *Inga* species were used less frequently than available, while *Trema*, *Alchornea*, Melastomataceae, and Lauraceae were used more frequently (Table 2). In Restoration, *Alchornea* was used less frequently than available and *Inga* spp., *Trema*, Other Trees, and Melastomataceae were used more frequently (Table 2).

During winter, both migrants and residents used a different distribution of plant species than the available distribution in both management systems, as measured by basal area and canopy cover (Table 2). In Production, for both residents and migrants, *Alchornea* was used more frequently, while *Inga* was used less often (Table 2). *Trema* was used more frequently by migrants in Production, but less often by residents (Table 2). In Restoration, *Trema* and Other Trees were used more frequently by both migrants and residents, while *Alchornea* and Melastomataceae were used less often (Table 2). Lauraceae was used more frequently by migrants in Restoration (Table 2). Substrate use by season and management system is summarized in Table 3. Vegetation and substrate use are evaluated in the shade and coffee layers separately.

RESIDENT AND MIGRATORY BIRDS.—For winter observations, multinomial logistic regression found significant differences between management system and migratory status with a higher proportion of residents observed foraging in Restoration than Production and vice versa for migrants (mlogit: $N = 1049$, $\chi^2 = 65.1$, $P < 0.00001$). However, evaluating birds by migratory status, there was no overall difference in the distribution of foraging observations of migrants and residents across layers, though resident birds foraged more frequently in the coffee layer than migrants in Restoration (Fig. 1; $df = 3$, $\chi^2 = 2.4$, $P = 0.49$). Both residents and migrants foraged more frequently in the shade layer and less in the coffee

TABLE 2. Distribution of avian foraging observations among different plant categories compared with expected distributions based on basal area and canopy cover in a Production and a Restoration coffee management system in Chiapas, Mexico. Methods describe plant categories and vegetation measurement in randomly placed plots. N = total number of foraging observations.

| | <i>Inga</i> spp. | <i>Trema micrantha</i> | Other Trees | <i>Alchornea latifolia</i> | <i>Schizolobium</i> Form | Melastomataceae | Lauraceae | Other | N | P for Overstory Basal Area | P for Canopy Cover Counts |
|--|------------------|------------------------|-------------|----------------------------|--------------------------|-----------------|-----------|-------|-----|----------------------------|---------------------------|
| Proportion of foraging observations on each plant category | | | | | | | | | | | |
| Production | | | | | | | | | | | |
| Summer | 0.62 | 0.19 | 0.05 | 0.02 | 0.01 | 0.05 | 0.05 | 0.01 | 292 | <0.0001 | 0.001 |
| Winter | 0.66 | 0.16 | 0.04 | 0.09 | 0.01 | 0.02 | 0.03 | 0.004 | 284 | <0.0001 | <0.0001 |
| Total | 0.64 | 0.17 | 0.04 | 0.06 | 0.01 | 0.03 | 0.04 | 0.007 | 576 | <0.0001 | <0.0001 |
| Restoration | | | | | | | | | | | |
| Summer | 0.45 | 0.14 | 0.11 | 0.06 | 0.08 | 0.1 | 0.05 | 0.02 | 408 | <0.0001 | <0.0001 |
| Winter | 0.34 | 0.09 | 0.19 | 0.19 | 0.1 | 0.04 | 0.06 | 0.002 | 431 | <0.0001 | <0.0001 |
| Total | 0.39 | 0.11 | 0.15 | 0.13 | 0.09 | 0.07 | 0.06 | 0.01 | 839 | <0.0001 | <0.0001 |
| Availability Proportions | | | | | | | | | | | |
| Basal Area | | | | | | | | | | | |
| Production | 0.77 | 0.07 | 0.01 | 0.04 | 0.000 | 0.0 | 0.0 | 0.1 | | | |
| Restoration | 0.23 | 0.0 | 0.1 | 0.62 | 0.02 | 0.004 | 0.03 | 0.0 | | | |
| Canopy Cover | | | | | | | | | | | |
| Production | 0.78 | 0.13 | 0.08 | 0.03 | 0.01 | 0.0 | 0.0 | 0.0 | | | |
| Restoration | 0.37 | 0.01 | 0.09 | 0.36 | 0.11 | 0.008 | 0.06 | 0.0 | | | |

layer in Restoration than Production (Fig. 1; $df = 3, \chi^2 = 36.9, P < 0.0001$).

SHADE LAYER.—Overall, birds in the shade layer were observed foraging most frequently in *Inga* trees (Table 2). The proportion of observations in *Inga* was higher in Production than Restoration, the other tree categories combined to make up a higher fraction of plant species visited by birds than *Inga* (Table 2; $df = 7, \chi^2 = 151.6, P < 0.0001$). For both summer and winter, there were significantly different distributions of plant species used between Production and Restoration (Table 2; summer: $df = 7, \chi^2 = 44.6, P < 0.0001$; winter: $df = 7, \chi^2 = 117.7, P < 0.0001$). Within each season, *Inga* and *Trema* had a higher proportion of observations in Production than Restoration, while *Alchornea*, *Schizolobium*, Lauraceae, Melastomataceae, and Other Trees had higher proportions in Restoration, but in summer, more than 50 percent of observations were in *Inga* or *Trema*. There were also significantly different patterns of plant species use by birds within each management system between seasons (Table 2; Production: $df = 7, \chi^2 = 20.1, P = 0.005$; Restoration: $df = 7, \chi^2 = 59.9, P < 0.0001$). In Production, *Trema*, Lauraceae, and Melastomataceae had more observations in summer, while *Inga* and *Alchornea* had more in winter. In Restoration, *Inga*, *Trema*, and Melastomataceae had more observations in summer, while Other Trees, *Alchornea*, *Schizolobium*, and Lauraceae had more in winter.

Birds did not use different foraging substrates in the two management systems (Table 3, $df = 7, \chi^2 = 13.1, P = 0.069$). During

summer, the distribution of foraging substrates was not significantly different between management systems ($df = 7, \chi^2 = 10.8, P = 0.15$), but during winter there was a significant difference (Table 3; $df = 7, \chi^2 = 16.8, P = 0.019$). Between seasons, there was a significantly different distribution of foraging substrates used (Table 3; $df = 7, \chi^2 = 76.4, P < 0.0001$). The foraging substrate distributions differed significantly between seasons for both management systems with a greater proportional use of fruit and air in summer and flowers and branch/twig in winter (Table 3; Production: $df = 7, \chi^2 = 37.8, P < 0.0001$; Restoration: $df = 7, \chi^2 = 53.4, P < 0.0001$).

Within the shade layer, there was a different pattern of food resource use between Production and Restoration with fruit taken more often in Restoration and more use of nectar in Production (Fig. 2; $df = 3, \chi^2 = 12.4, P = 0.0062$). By season, there was no difference between management systems in resources taken during summer ($df = 3, \chi^2 = 6.3, P = 0.1$), but there was a significant difference during winter ($df = 3, \chi^2 = 13.4, P = 0.0039$). The pattern of resource use was also different between seasons with a higher proportion of arthropods and fruit taken during summer and a higher proportion of nectar taken in winter (Fig. 2; $df = 3, \chi^2 = 141.8, P < 0.0001$). Both management systems differed significantly in resource use between seasons with greater use of fruit during the summer and nectar in winter (Fig. 2; Production: $df = 3, \chi^2 = 80.3, P < 0.0001$; Restoration: $df = 3, \chi^2 = 67.0, P < 0.0001$). Arthropod use was only different between seasons in Production (Fig. 2). There were also significant differences in food resource use seasonally across shade-tree categories (Fig. 3; mlogit

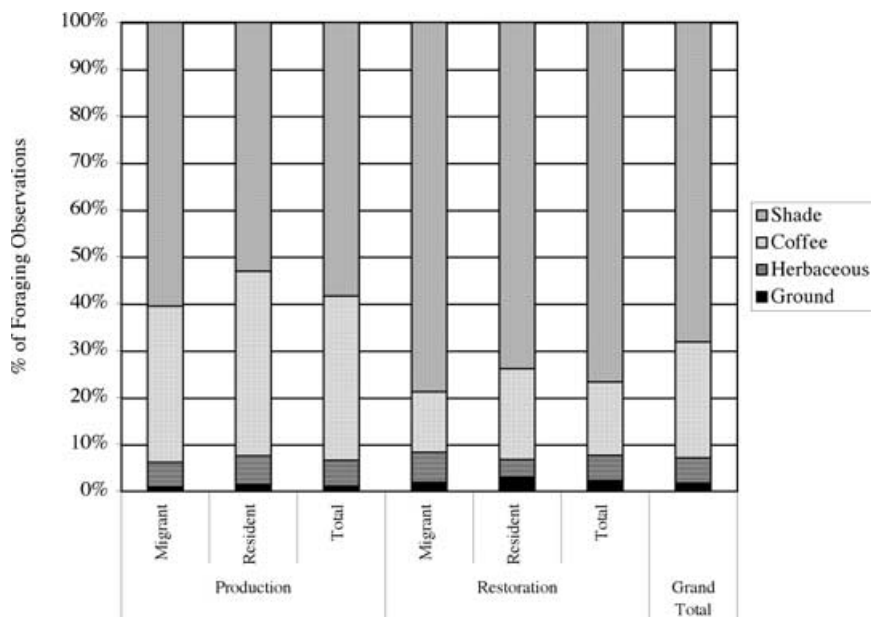


FIGURE 1. Proportion of foraging observations of resident and migratory birds in each vegetative layer in each coffee management system during winter dry season.

Tree group: $df = 9, \chi^2 = 1671, P < 0.0001$; Seasons: $df = 2, \chi^2 = 864, P < 0.0001$; Interaction: $df = 5, \chi^2 = 895, P < 0.0001$).

COFFEE LAYER.—In the coffee layer, most foraging was observed in coffee plants with marker plants a distant second ($N = 445$, *Coffea arabica*: 82.2%, Marker Plants: 12.6%, Other categories: 5.2%). No significant differences were found in plant species used between management systems ($df = 4, \chi^2 = 1.59, P = 0.81$), but there was a significant difference between seasons with a greater use of marker plants during summer than winter ($df = 4, \chi^2 = 27.4, P < 0.0001$). Birds also foraged in different foraging substrates in the two management systems with a higher proportion of branch/twig and flower in Production and a higher proportion of leaf and air in Restoration ($df = 7, \chi^2 = 15.0, P = 0.036$). Between seasons, foraging substrates also differed with a higher proportion of flowers

in summer and a higher proportion of leaf, branch/twig, and air during winter ($df = 7, \chi^2 = 34.3, P < 0.0001$).

No difference in food resources used was found between management systems for both seasons combined (Combined%: Arthropoda 73.1%, Nectar 25.8%, Fruit 1.1%; $df = 2, \chi^2 = 1.77, P = 0.41$). In Production, there was a higher proportion of nectar and lower proportion of arthropods taken during summer than winter ($df = 2, \chi^2 = 7.42, P = 0.024$). In Restoration, there was no difference in resources used between seasons ($df = 1, \chi^2 = 0.52, P = 0.47$). Of the 202 prey items taken in the coffee layer in both management systems, only three were fruit, two from *C. arabica*.

INSECTIVORY.—Overall, more arthropods were taken as prey items by birds in winter than summer ($N = 1044$; summer 45.4%, winter 54.5%; $\chi^2 = 8.65, P = 0.003$) and in Restoration than Production ($N = 1044$; Production 46.9%, Restoration 53.1%; $\chi^2 = 3.92,$

TABLE 3. Proportion of avian foraging observations using different substrate types across seasons and management systems in Chiapas, Mexico. Foraging substrate types and management systems described in Methods.

| Season | Management System | Leaf | Branch /twig | Fruit | Air | Flower | Special Leaf | Trunk | Other | N |
|-------------|-------------------|------|--------------|-------|------|--------|--------------|-------|-------|------|
| Summer | Production | 0.41 | 0.26 | 0.12 | 0.08 | 0.07 | 0.02 | 0.03 | 0.02 | 410 |
| | Restoration | 0.43 | 0.17 | 0.17 | 0.11 | 0.04 | 0.02 | 0.03 | 0.02 | 528 |
| | Total | 0.42 | 0.21 | 0.15 | 0.1 | 0.054 | 0.02 | 0.03 | 0.02 | 938 |
| Winter | Production | 0.44 | 0.26 | 0.05 | 0.09 | 0.101 | 0.03 | 0.03 | 0.01 | 524 |
| | Restoration | 0.4 | 0.25 | 0.08 | 0.1 | 0.101 | 0.05 | 0.02 | 0.01 | 596 |
| | Total | 0.42 | 0.25 | 0.06 | 0.1 | 0.101 | 0.04 | 0.03 | 0.01 | 1120 |
| Grand Total | | 0.42 | 0.23 | 0.1 | 0.1 | 0.08 | 0.03 | 0.03 | 0.01 | 2058 |

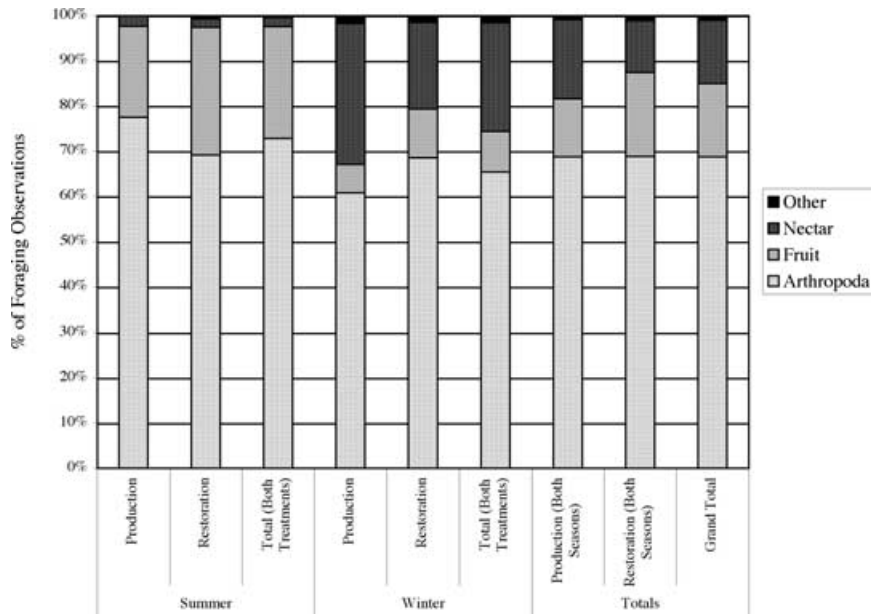


FIGURE 2. Proportion of resource use by birds in the shade layer by management system and season.

$P = 0.048$). The seasonal pattern was the same for the coffee layer ($N = 245$; summer 32.7%, winter 67.3%; $\chi^2 = 29.5$, $P < 0.0001$), but more arthropods were taken in Production than Restoration ($N = 245$; Production 62.9%, Restoration 37.1%; $\chi^2 = 16.2$, $P < 0.0001$). For the coffee layer, these differences were also significant for each management system between seasons, but the difference between management systems was driven by the significant difference in the winter ($N = 165$, Production 64.2%, Restoration 35.8%; $\chi^2 = 13.4$, $P = 0.0003$). For coffee plants only, the same

patterns of insectivory were observed. In the shade layer, there were more arthropods taken in Restoration than Production ($N = 748$; Production 42.1%, Restoration 57.9%, $\chi^2 = 18.6$, $P < 0.0001$), mostly due to the high number of arthropods taken in Restoration during winter ($N = 386$; Production 37.8%, Restoration 62.2%; $\chi^2 = 22.9$, $P < 0.0001$). For the shade layer within Restoration, winter was significantly higher than summer ($N = 433$; summer 44.6%, winter 55.4%; $\chi^2 = 5.10$, $P < 0.024$). The opposite trend was observed with *Inga* trees, where fewer arthropods were taken

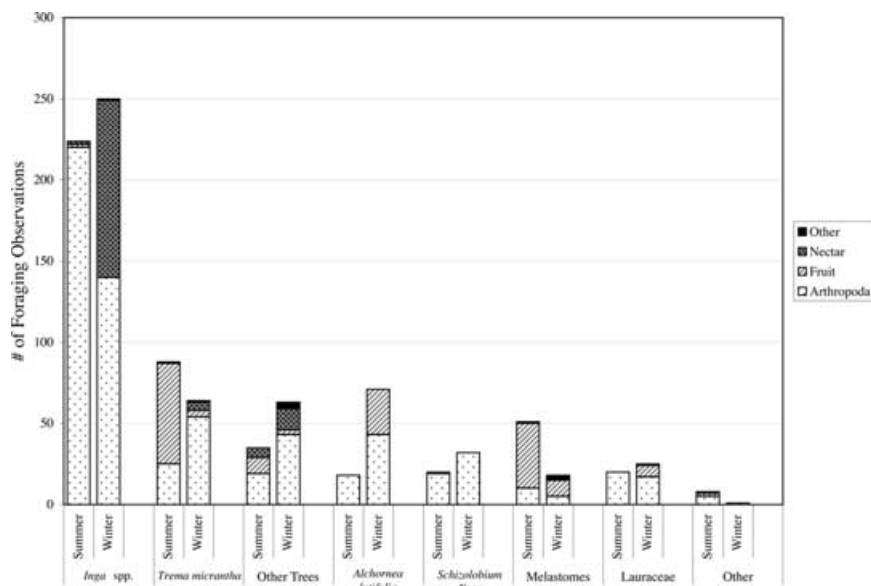


FIGURE 3. Number of foraging observations for all birds showing resource use in each shade tree category for each season.

during winter ($N = 388$; summer 60.8%, winter 39.2%; $\chi^2 = 18.2$, $P < 0.0001$), mostly due to low insectivory in Restoration. Also in *Inga* trees, more arthropods were taken during winter in Production than Restoration ($N = 152$; Production 59.9%, Restoration 40.1%; $\chi^2 = 5.92$, $P = 0.015$).

Birds took lepidopteran prey more frequently during summer than winter ($N = 127$; summer 78.0%, winter 22.0%, $\chi^2 = 39.7$, $P < 0.0001$), but there were no differences between management systems (Production 54.3%, Restoration 45.7%, $\chi^2 = 0.95$, $P = 0.33$). Most lepidopteran prey were taken from the shade layer (107 observations of 127 total) and larvae were the life stage most frequently taken (106 larvae, 17 adults, 3 stage not recorded, 1 pupa). In the coffee layer, there was no seasonal difference in frequency of lepidopteran prey, but the sample size was low ($N = 13$, $\chi^2 = 0.69$, $P = 0.41$).

DISCUSSION

In this study, foraging behavior of birds varied significantly between seasons and between coffee management systems. A higher diversity of birds was found in the less-intensive management system (Restoration: 80 species, Production: 59 species). In addition, bird species richness was higher for both management systems during the winter with 27 long-distance migratory species observed, 23 and 21 species in Restoration and Production, respectively. During winter observations, a higher diversity and proportion of resident birds were observed foraging in the less-intensive system (Restoration: 40 species, Production: 27 species). Shade canopy vegetation grown by the two coffee management systems differed significantly with greater canopy cover and floristic diversity in Restoration than Production (Table 1), though the vegetative profile was similar (Dietsch 2003). This matches the pattern of greater avian diversity and abundance with increasing vegetative complexity found by other authors for coffee agroecosystems (Wunderle & Latta 1996; Greenberg *et al.* 1997a,b; Calvo & Blake 1998; Dietsch 2003). The significant patterns in overall bird community foraging dynamics found by this study suggest that increased floristic diversity provides additional resources that may allow a greater diversity of birds to coexist in less-intensively managed coffee agroecosystems.

SHADE LAYER.—As observed in other studies, the majority of foraging observations occurred in the shade layer for both management systems (Greenberg *et al.* 1997a, Wunderle & Latta 1998, Dietsch 2003). Birds used a more even distribution and greater diversity of shade tree species in Restoration than Production (Table 2). With few opportunities to change management practices in the coffee layer, shade-grown coffee certification efforts have focused on shade management practices that may benefit birds. An evaluation of vertical stratification by birds in these management systems suggests that the greater floristic diversity of shade trees in Restoration also contributes to higher avian diversity (Dietsch 2003; also see Greenberg 1997a). There is a strong seasonal signal to resource use associated with particular tree species groups (Fig. 3). The greater proportion of frugivory found in Restoration suggests that addi-

tional fruiting resources may be one mechanism contributing to the avifauna. Though many of the forest trees augmenting this system are still not mature enough to produce fruit, some species, including several Lauraceae, are beginning to bolster the diversity of available fruit resources birds are using (Fig. 3). Additional tree species in Restoration may increase foraging opportunities for flycatchers, perhaps through a greater variety of perches or increased abundance of flying insects. Both frugivores and flycatchers show increased diversity in Restoration (T. V. Dietsch, pers. obs.; see Table S1 for complete bird list).

Both methods for determining tree species available for foraging had bias problems particularly in estimating proportions of some tree species due to differences in tree growth patterns. *Alchornea*, for example, tends to produce disproportionately large trunks compared to actual tree height, and the bias associated with use of basal area may be unacceptably large. The canopy method also has some bias problems: cover of *Schizolobium* and a few others species were probably overestimated because of their high and arching but thin canopies. Adjusting this method to record all species above each point might give a better estimate of available foraging habitat for each tree species (or group), though total coverage would then be greater than 1 due to overlap.

COFFEE LAYER.—Wunderle and Latta (1998) reported that almost all foraging maneuvers in coffee were associated with insectivory. In this study, the majority of observations in the coffee layer was similarly of insectivory although over a quarter of observations were nectivorous. This study supported anecdotal observations that birds are not significant predators of coffee berries, perhaps due to the alkaloids found in berries.

The relatively homogenous coffee layer was principally composed of coffee bushes and plants used to mark parcels within the plantation (Marker Plants). Many marker plants on this farm, especially *Sanchezia nobilis*, produce flowers year-round and provide an important nectar source for hummingbirds. There was greater use of marker plants during summer than winter. This is reflected in resources taken; there was a higher proportion of nectar and lower proportion of arthropods taken during summer than winter in Production. Production has a higher abundance of hummingbirds (Dietsch 2003) with a more open canopy and greater abundance of flowers (T. V. Dietsch, pers. obs.). These results suggest that there may be conservation alternatives in the understory that could improve resource availability for forest-associated understory birds. In this case, sparsely located (~25 m) flowering plants helped boost hummingbird populations. Similar options may be available for frugivores and insectivores.

FRUGIVORY AND NECTIVORY.—Resource use shifted seasonally by shade tree species (Fig. 3). Though this study did not measure the resources available in each tree species, seasonal changes in availability can be inferred from usage. For example, birds used only arthropod prey in *A. latifolia* during summer, but in winter when *A. latifolia* fruited the number of foraging observations increased fourfold with 39 percent of these being on fruits (Fig. 3). *Trema*, Melastomaceae, and Other Trees provided fruit during summer,

while *Alchornea* and Lauraceae were important winter fruit sources. In contrast, there were few sources of nectar in shade canopy during summer, while in winter *Inga* flowers were used abundantly, as mentioned previously. This break in the phenology may represent a bottleneck for some nectarivores. During summer, most nectarivores were observed foraging in the coffee or herbaceous layer.

Tree diversity has been used as an indicator of the likelihood of year-round resource availability with greater diversity implying more complete phenologies. Though shade tree species richness has broad application throughout the tropics as a general indicator of improved resource availability to address phenological bottlenecks, a better understanding of the role of composition is necessary to tailor farmer outreach programs to address regional conservation needs. Resources provided by epiphytes should also be considered in evaluating resource phenology. Shade-coffee plantations with epiphytes maintained higher abundance and diversity of the inhabitant bird fauna than plantations without epiphytes (Cruz-Angon & Greenberg 2005). Identifying keystone tree and epiphyte species is a critical area of research for future conservation efforts in coffee and other managed ecosystems.

INSECTIVITY.—Overall, there are strong seasonal patterns in insectivory with greater foraging in the coffee layer during winter. Insects may be less abundant in the winter season due to dry, hot conditions and reduced availability of some vegetative resources (e.g., increased loss of leaves, reduction in fruiting and flowering for some plant species). Many insect species are dormant during some winter months, or may retreat to lower shaded vegetation. Birds also respond to hot, dry conditions and shifts in prey by changing their foraging behavior. Birds may move down from the canopy at midday as a response to increased temperature (Walther 2002). If this is a response to hot conditions in the upper canopy during midday, the cumulative effect of more hot days during the dry season may lower average foraging heights in winter.

Similarly, during winter, greater insectivory in the coffee layer of Production than Restoration may result from shifts in avian foraging behavior. This hypothesis would be supported if arthropod abundances were consistent between management systems. In a Jamaican coffee plantation, Johnson (2000) found no difference in the arthropod abundances of coffee grown under different shade tree species or shade densities. Arthropod abundance was seven times lower than in the shade layer, but insecticide use in the coffee layer may have kept artificially low (Johnson 2000). Nonetheless, coffee plants may naturally produce the same effect due to the presence of alkaloid compounds that may reduce herbivory (Frischknecht *et al.* 1986).

Birds took more arthropods in the shade layer of Restoration during winter but not overall or in Production. This may result from a different species composition of trees in the shade layer of each management system, in particular, the greater abundance of *Inga* in Production. Birds took fewer arthropods in *Inga* trees during winter than summer. This reduction, possibly due to leaf loss and harsh microclimatic conditions from pruning, may have been

ameliorated somewhat during the period of this study because *Inga* trees were in flower attracting numerous insects to the nectar-rich flowers, though many Hymenoptera attracted would not constitute typical prey for insectivores (T. V. Dietsch, pers. obs.). The greater diversity of shade trees in Restoration may offer greater refuge from climatic conditions in the shade layer, while insects in Production have fewer options and may retreat to the coffee layer. A better understanding of overwintering (dry season) habits of insects in this region, especially in relation to coffee management practices, may help explain foraging patterns of insectivorous birds.

In Jamaica, Johnson (2000) found fewer arthropods in shade trees growing in less-densely shaded areas, which corresponded with lower avian abundances. In his study, denser areas were associated with *Inga* trees, which also supported higher abundances of arthropods than the other main shade tree in his study, *Pseudalbizia*. Other authors have also noted that *Inga* supports high arthropod abundances (Greenberg *et al.* 1997a,b; Wunderle & Latta 1998).

During summer months, when daily afternoon rains may minimize microclimatic differences, there were no differences in insectivory between management systems. Differences in insectivory between management systems should be viewed with caution because numbers of arthropod prey taken in particular plant species (e.g., coffee plants or *Inga* trees) may not represent sizeable reductions in the per plant insect load.

Birds took lepidopterans as prey items more frequently during the summer. There was no difference in lepidopterans taken between management systems for each season. The increased use of lepidopterans in summer may be due to an increased abundance of larvae during the rainy season, which corresponds with resident breeding seasons. Birds feeding young may preferentially select these larvae as an important energy resource for growing juveniles (Greenberg 1981, 1995). This selectivity may explain why residents forage higher in Production during the summer (Dietsch 2003). Lepidopteran larvae may be rare on coffee plants due to the alkaloid-rich leaves that suppress herbivores (Frischknecht *et al.* 1986). Consequently, there may be shifts in avian foraging behavior related to insect life-stage phenologies.

MANAGEMENT IMPLICATIONS.—The augmentation of the restoration management system with native forest trees seems to provide additional resources than may be attractive to forest-associated birds. Additional research on foraging behavior within local unmanaged forests could confirm this hypothesis and help identify other important trees for the forest avifauna. Though shade-grown coffee certification does not require the use of particular tree species, there is a requirement to maintain tree species diversity at a relatively high level. Encouraging growers to plant and maintain locally important native trees in the shade canopy is an important component of shade-grown coffee certification outreach efforts (Greenberg & Rice 2000, Rice & Drenning 2003). Identification and use of forest tree species that provide biologically important resources, including nesting and foraging opportunities (*i.e.*, fruit, flowers, and significant arthropod populations), may improve these outreach efforts

and the conservation benefits produced from the resulting coffee agroecosystems.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online at: www.blackwell-synergy.com/toc/btp
Table S1

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