Biodiversity and Conservation **13:** 2419–2441, 2004.

Characteristics of bird species using forest and agricultural land covers in southern Costa Rica

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Received 29 October 2002; accepted in revised form 18 August 2003

Key words: Agroecosystem, Antbirds, Coffee, Costa Rica, Deforestation, Logistic regression, Pasture, Tropical forest

Abstract. Our understanding of why tropical forest species differ in their ability to inhabit agroecosystems is limited, despite the link between this ability and the likelihood of population decline for species inhabiting regions undergoing widespread conversion of forest to agriculture. We used logistic regression and data from southern Costa Rica to develop a model based on natural history characteristics to distinguish between forest species that did or did not use agricultural land covers. We sampled birds along 15 3.0-km routes, seven in forest and eight in agriculture, five times over three years. Each species was classified as an F-species, detected only in forest, a G-species, detected in both forest and agriculture, or an A-species, detected only in agriculture. Thirty percent of species were F-species, 42% were G-species, and 28% were A-species. Based on the logistic regression model, the likelihood of being a G-species, as opposed to an F-species, was low for species that were dependent on forest interior, had a stenophagous diet, and a small elevational range. Weight, resident versus migrant status, and whether or not a species was insectivorous, were not significant predictors of being a G-species. For all F–G species pairs, the model correctly predicted the G-species 70% of the time. The model provides a first step in identifying those characteristics that predispose forest species to use agricultural land. In addition, our results indicate that the structurally simple agricultural systems of the study region are of limited value for a large proportion of the regional species pool.

Introduction

The conversion of forest to agricultural land covers is occurring at rapid rates in many tropical areas (Houghton 1994; Skole et al. 1994), with potentially profound effects on the biodiversity of these regions (Wilson 1992). These land-cover trends have spurred research to investigate the role that agroecosystems play in providing habitat for tropical organisms and in the conservation of biodiversity (e.g., Estrada et al. 1997; Greenberg et al. 1997a; Moguel and Toledo 1999; Roberts et al. 2000; Ricketts et al. 2001; Petit and Petit 2003). Although some tropical areas like the Dominican Republic (Wunderle and Latta 1996) and southern Mexico (Greenberg et al. 1997b) still maintain some forest-like agroecosystems, such systems have all but disappeared from other areas (Perfecto et al. 1996). In our study region, for example, the cantón of Coto Brus in southern Costa Rica, nearly all agroecosystems, primarily coffee and pasture, are structurally very simple. Research to distinguish the types of species that are able to use these agricultural land covers from those that are not, contributes to our being able to predict those species that are likely to be little affected by widespread forest conversion to structurally simple agroecosystems and those species that will likely experience population declines.

Our focus here is on species that inhabit forest and which we will refer to as forest species throughout the paper. Although forest species display a range of responses with regard to their use of agricultural habitats, for our purposes we will consider each forest species as falling into one of two groups: (1) forest specialist species, those that rarely use land covers other than mature forest, and (2) forest generalist species, those that regularly use mature forest and agricultural land covers. We exclude from detailed consideration those species that rarely use forest and typically inhabit land covers such as grasslands, crop fields, and young second growth.

Previous work suggests that particular characteristics may be linked to a low likelihood of a tropical forest species using agricultural land covers, including relatively large size (Thiollay 1995), dependence on forest interior as opposed to forest canopy and/or edge (Terborgh and Weske 1969; Andrade and Rubio-Torgler 1994; Thiollay 1995; Petit and Petit 2003), being an insectivore (Bowman et al. 1990; Johns 1991; Thiollay 1995; Canaday 1996; Raman et al. 1998; but see Andrade and Rubio-Torgler 1994), and/or having a specialized mode of searching for food (Terborgh and Weske 1969). Given that a number of latitudinal migrant species have been shown to use several habitat types on their wintering grounds (e.g., Wunderle and Waide 1993; Confer and Holmes 1995; Conway et al. 1995; Johnson and Sherry 2001), we suspect that resident species may be less likely to use agricultural land covers than migrants. A recent review also suggests that specialist, forest interior, and non-migratory species are more likely to be behaviorally inhibited from crossing barriers such as matrix (agricultural) habitat compared to generalist, forest canopy, and migratory species (Harris and Reed 2002).

In addition to these empirical results, theory suggests that organisms inhabiting less frequently disturbed areas with more benign abiotic conditions (e.g., tropical forest), compared to more frequently disturbed areas with less benign abiotic conditions (e.g., agricultural systems), are likely to be more specialized and demonstrate a narrower range of environmental tolerance (Grime 1977; Greenslade 1983; Southwood 1988).

Based on these empirical and theoretical considerations we conducted an exploratory analysis to determine whether we could develop a model that used natural history characteristics to differentiate between forest specialist species and forest generalist species. Such a model would allow us to distinguish between species that would be able to maintain viable populations in areas with extensive conversion of forest to simple agricultural land covers and species that would be restricted to remaining forest. Our results are also likely to indicate which species are likely to be least and most at risk of decline in forest fragments. Tropical bird species differ in their likelihood of sustaining populations in tropical forest fragments (Kattan et al. 1994; Stouffer and Bierregaard 1995) and these differences are, in part, attributable to differences in the extent to which forest species use agricultural matrices surrounding forest fragments (Sekercioglu et al. 2002).

The majority of the data collection took place on the Pacific slope of the Talamanca Mountains, much of which is part of the Amistad Biosphere Reserve. The Reserve contains the largest unbroken tract of montane forest in Central America (MAB 1990) and has been designated by the World Wildlife Fund as one of the 'Global 200', one of the 233 most valuable ecoregions on Earth in terms of diversity of species and ecological processes (Olson and Dinerstein 1998). However, despite the significance of the area, information on biodiversity and effects of land-cover change is limited (e.g., Sisk 1992; Lips 1998; Holl 2002; Lindell and Smith 2003), and forest conversion to agricultural land covers threatens to substantially diminish the biodiversity of the region before it has even been well documented.

We use the term land cover or land-cover types to distinguish areas that would be classified differently from other areas based on observations of the vegetation structure. We use the term habitat to imply that a land-cover type has resources important to particular organisms. We use forest interior to describe that habitat within forest below the canopy layer of vegetation (Stiles 1985). We assume that the microclimate of this habitat is substantially different from that of the canopy in having less light and less variable moisture and temperature regimes.

Methods

Study area

Costa Rica is in the Mesoamerica 'hotspot', defined by Myers et al. (2000) as a region with high numbers of endemic species and high rates of habitat loss. Although deforestation rates in Costa Rica had begun to decelerate by the mid-1980s, the majority of the country's forest had been converted to other land-cover types by 1991 (Sánchez-Azofeifa 1996). Our study region, the Coto Brus cantón in the province of Puntarenas in southern Costa Rica, has experienced substantial conversion of forest to coffee plantations and pasture (Manger 1992) and has lost approximately 81% of its original forest cover (Sánchez-Azofeifa 1996).

The plantations and pasture that have replaced forest in much of Costa Rica have few structural similarities to primary forest. By the early 1990s 40% of the area devoted to coffee production in Costa Rica had been converted from more rustic types of plantations with large shade trees to more 'technified' plantations with short (3–7 m) trees or no trees (Rice and Ward 1996). Today, traditional plantations with forest-level canopies are rare in our study region while technified plantations are an important land-cover type, along with cattle pasture.

Data collection

We sampled the bird species along 15 3.0-km routes in the vicinity of three sites, Las Alturas, Mellizas, and San Vito. All sites were within an approximately 35-km diameter area, surrounding the Coto Brus Valley, at approximately 8°50′ N, 82°55′

Table 1. Approximate elevations covered over routes.

Agricultural route	Low elevation (m)	High elevation (m)	Forest route	Low elevation (m)	High elevation (m)
CERR	1300	1550	TUTI	1200	1550
COTO	1300	1500	ECHA	1500	1700
FILA	1200	1450	WILS	950	1200
LECH	1250	1450	HILL	1400	1600
MELL	1250	1400	ELSA	1300	1650
PROG	1150	1200	SINN	1100	1150
RION	1000	1100	REDG	1500	1550
HOSP	900	1050			

W. Eight of the routes were in agricultural land covers and seven were in forest. All routes were located between 900 and 1700 m elevation (Table 1). Four routes were established at Las Alturas; six around Mellizas; and five around San Vito (Figure 1). The general vicinity of each forest route was chosen on the basis of access to forest by a dirt road or trail.

We randomly selected a number between 0 and 250 to determine the location of the first point per route. The number selected designated the number of paces from the point at which appropriate land cover for a route began, that is, at least 100 m from a forest edge into forest for the forest routes and at least 200 m from any other route. No overlap existed between routes.

One hundred and ninety-four points were sampled, divided among the 15 routes, with 9–15 points per route. Ninety-five of the points were in agricultural land-cover types and 99 were in forest. All points were at least 200 m apart. Vegetation at each point was categorized for each of four quadrants surrounding the point into the following categories: (1) residential, (2) pasture, (3) pasture with trees, (4) sun coffee, (5) mixed agriculture, (6) young second growth, (7) second-growth forest dominated by large trees or mature forest, and (8) other. For the forest routes, all points were in category 7. For the agricultural routes, all points were in categories 1–6 or 8. Proportions of different land-cover types sampled along the agricultural routes are in Table 2. Detailed plot-level vegetation data from the study region are available in Holl (1999; forest and pasture) and Lindell and Smith (2003; forest and coffee).

We used 50-m fixed radius sampling plots for the point counts and they lasted 6 min. Counts were conducted between sunrise and 10 A.M. on clear days with little or no wind. Nocturnal species are not considered here. All species seen or heard within 50 m were recorded. All counts were conducted by J.R.Z., who has numerous years' experience conducting point counts in Costa Rica. Sampling took place five times: in February and early March 1998 and 1999 and in late July, August, and early September of 1998, 1999, and 2000.

At seven of the 15 routes we used mist nets to supplement the point-count data and to assess the types of species likely to be present but unlikely to be detected by point counts (Rappole et al. 1993). Netting was conducted near one point along each of the seven routes for one morning in the February and August periods of

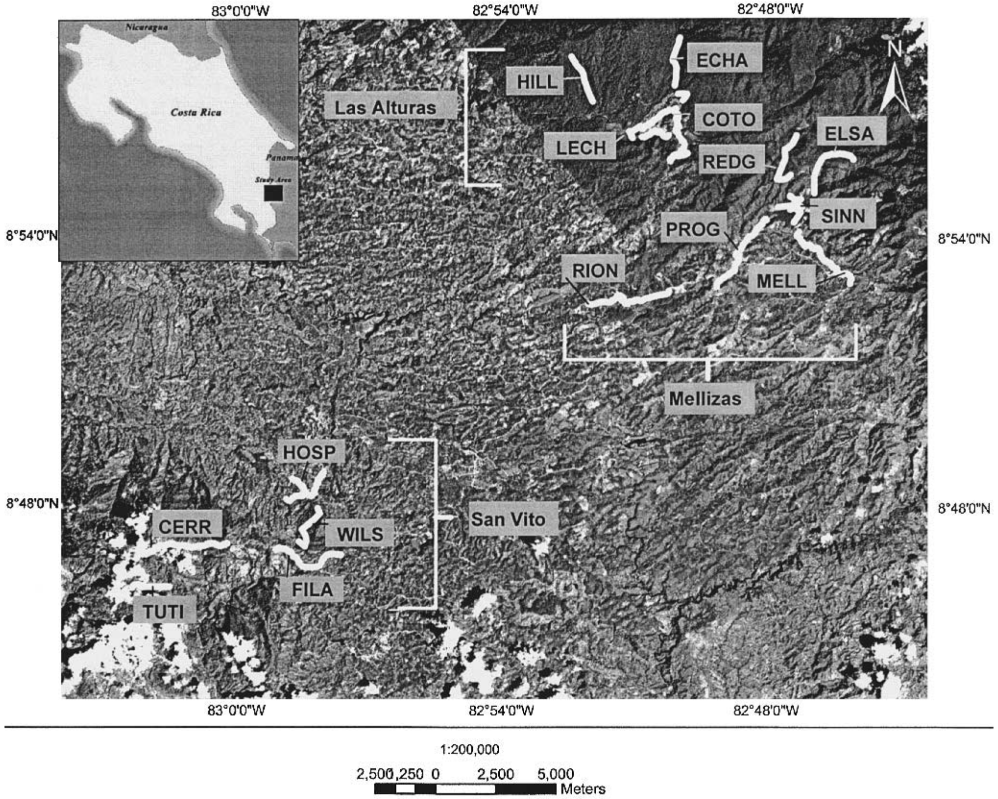


Figure 1. Landsat 7 image of the study area in southern Costa Rica centered on Valle de Coto Brus. Bold white lines are sampling routes. The darkest gray areas are forest. Lighter shades are pasture, coffee plantations, and other land-cover types. For example, the ECHA route is in forest and the HOSP route is primarily in agriculture. The Las Tablas Protected Area, an extensively forested part of the Amistad Biosphere Reserve, is located in the upper right corner of the figure.

Table 2. Proportions of major land-cover types sampled along agricultural routes. Proportions were calculated based on descriptions of the land covers in each of four quadrants surrounding each sampled point. The number of quadrants of each land-cover type was divided by the total number of quadrants per route.

Route	Residential	Pasture	Pasture with trees	Sun coffee	Mixed agriculture	Young second growth	Other
CERR	0.00	0.48	0.33	0.00	0.00	0.20	0.00
COTO	0.11	0.11	0.36	0.00	0.42	0.03	0.00
FILA	0.07	0.57	0.20	0.02	0.13	0.15	0.02
LECH	0.00	0.33	0.39	0.00	0.11	0.17	0.00
MELL	0.19	0.02	0.00	0.08	0.48	0.21	0.02
PROG	0.23	0.11	0.02	0.07	0.41	0.15	0.02
RION	0.05	0.04	0.00	0.11	0.64	0.09	0.07
HOSP	0.27	0.21	0.21	0.00	0.23	0.08	0.00

1998 and 1999 for a total of four sampling days per point. We used 10 nets with 30 mm mesh. Three of the mist-net points were in forest and four were in or at the edge of coffee plantations. Netting took place on days with little or no wind or rain and nets were open for 6 h, beginning soon after sunrise. We combined data from the four sampling periods and so have a total of 120 net-hours per point. At each point the nets were arrayed end to end in a line, except for one point where nets were arrayed in one set of four nets and three sets of two nets.

Data analysis

Each species detected was categorized as an F-species, detected only in forest land covers over all sampling periods (forest specialist species), a G-species, detected in both forest and agricultural land covers (forest generalist species), or an A-species, detected only in agricultural land covers. For the purposes of the model-building exercise we considered only the F- and G-species.

We used logistic regression to determine the most appropriate model for distinguishing the F- and G-species. Based on the empirical and theoretical considerations discussed earlier, the initial independent variables we used to build the model included two continuous variables, (1) weight (WEIGHT) and (2) elevational range (ELEVATION), and four categorical variables: (3) whether a species is strictly insectivorous or not (INSECT), (4) diet breadth (STENOPHA), (5) migratory status (LATIMIGR), and (6) the dependence of a species on forest interior (FORINT). The response variable was the probability of being a G-species.

Weight was used as a measure of body size and species' weights were taken from Stiles and Skutch (1989) with a mean weight calculated if males and females differed. Elevational range was used as a measure of tolerance of environmental conditions, with a greater range assumed to mean greater tolerance. Ranges were taken from Stiles and Skutch (1989) and Stotz et al. (1996). If the ranges from these two sources differed we used the greater of the two.

Information on foraging behavior was taken from Stiles and Skutch (1989) and Karr et al. (1990) in order to classify species as strict insectivores or not and as stenophagous or not (diet breadth). Strict insectivores were reported to eat only insects while stenophagous species ate only one type of food (invertebrates, fruits with seeds, vertebrates, grass seeds, or nectar, as opposed to some combination of these types). For seven hummingbird species (*Amazilia decora, A. edward, Campylopterus hemileucurus, Elivra chionura, Lampornis castaneoventris, Colibri thalassinus, and Eupherusa eximia*), we could not find documentation as to whether or not they included invertebrates in their diet. We considered these seven species to include invertebrates based on data from congeneric species (Kuban and Neill 1980; Karr et al. 1990; Hayes et al. 2000) and the likely widespread use of invertebrates by hummingbirds (Stiles 1995).

We classified species with regard to dependence on forest interior based on data presented in Stiles (1985). We used three categories: (1) dependent on non-forest habitats and not using forest edge and/or canopy, (2) using forest habitats including forest edge and/or canopy, and (3) dependent on forest interior and not using forest edge and/or canopy. Species were classified as latitudinal migrants or not based on information from Stiles and Skutch (1989).

We followed the model-building techniques described by Hosmer and Lemeshow (2000) to build a logistic regression model to predict the likelihood of being a G-species. We also used a stepwise logistic regression procedure (SAS 2001) and then compared results from the model we built and that which resulted from the stepwise procedure. For the stepwise procedure we used initial significance levels of $P = 0.25$ to enter the model and $P = 0.25$ to stay in the model, to capture any variables that may have contributed to the likelihood of a species being a forest generalist, as opposed to a forest specialist. With both methods we determined whether the variables selected by ourselves or the SAS program should remain in the final model, and whether any interaction variables should be added to the final model, by conducting likelihood ratio tests between models with and without each particular variable (Hosmer and Lemeshow 2000). Likelihood ratio tests compare log likelihoods to generate a chi-square statistic that can be used to assess whether a particular variable contributes to a model. We also examined AIC values of candidate nested models as another criterion to choose the final best model. We examined the results of goodness-of-fit tests to determine whether a lack of fit existed between the data and the final models. We also report the results of the concordance of model predictions with actual observations.

Initial univariate analyses to test for differences between F- and G-species were conducted with *t*-tests for the continuous variables and *G*-tests for the categorical variables. For all *G*-tests of independence we employed Williams's correction (Sokal and Rohlf 1995). We assessed whether the distributions of the number of species detected per family detected differed for the F- and G-species groups with a Kolmogorov–Smirnov two-sample test (discussed below). Species and family assignments follow the American Ornithologist's Union (AOU 1998, 2000, 2002) check-list and supplements.

We also used Kolmogorov–Smirnov two-sample tests to determine whether the distributions of the number of species detected per family differed between the mist-net and point-count samples at the seven points where both techniques were used. The Kolmogorov–Smirnov test takes into account differences in location, dispersion, and skewness of two distributions. When the test is used for categorical variables and standard tables of critical values are used, the test is conservative (Sokal and Rohlf 1995). For these mist-net and point-count comparisons, we used a sequential Bonferroni procedure to adjust for the increased probability of observing statistical significance for any single test when multiple tests of the same hypothesis are conducted (Rice 1989).

Results

During the point counts, 11 788 individuals were counted of which 11 564 or 98.1% were identified to species. Of the 224 registrations that were not identified to species, 150 or 67.0% were unidentified hummingbirds. During netting we captured 979 individuals, 973 or 99.4% of which were identified to species (six individuals escaped before identification).

Of the 271 species detected over all sampling periods through the point counts and netting, 81 (29.9%) were F-species, 114 (42.1%) were G-species, and 76 (28.0%) were A-species. A complete list of the species detected is available from the first author.

Twenty-nine families of birds were represented in the 81 F-species and 27 families were represented in the 114 G-species. The distributions of the number of species within different families varied between the F- and G-species (Kolmogorov–Smirnov two-sample test, $P < 0.005$, $n = 195$). In some families the majority of species were F-species, including the trogons (5/6) and the antbirds (thamnophilids and formicariids, 10/12 species). These same patterns also exist for these families when considering detections: only 1 of 81 detections of trogons was in an agricultural land cover and only 3 of 545 detections of antbirds were in agricultural land covers. In other families the majority of species were G-species, including the thrushes (turdids, 6/6), the warblers (parulids, 13/22) and the tanagers (thraupids, 15/26; Table 3, Figure 2).

Initial univariate analyses, as suggested by Hosmer and Lemeshow (2000), showed that the six variables of interest differed to varying degrees between the F- and G-species, in the expected directions. All sample sizes for the following comparisons are 195. F-species showed a trend of being larger than G-species (143 ± 483 (SD) and 64 ± 179 g, respectively), although the difference was not significant at the $P = 0.05$ level ($t = 1.40$, $P < 0.10$). Elevational range was less for F-species compared to G-species (1975 ± 638 and 2171 ± 589 m, respectively, $t = -2.21$, $P < 0.05$). F-species were more likely to be highly dependent on forest interior than G-species (14.8% of F-species and 1.8% of G-species; $G = 14.12$, $\mathrm{df} = 2$, $P < 0.001$) and were less likely to be latitudinal migrants than G-species (4.9% of F-species and 14.0% of G-species, $G = 4.49$, $\mathrm{df} = 1$, $P < 0.05$). F-species

Table 3. Number of species within different families for F-, G-, and A-species groups.

Family	No. of F-species	No. of G-species	No. of A-species
Tinamidae	1	1	0
Ardeidae	0	0	1
Cathartidae	0	0	1
Accipitridae	3	0	2
Falconidae	0	1	1
Cracidae	2	1	0
Odontophoridae	1	0	0
Rallidae	0	0	3
Eurypygidae	1	0	0
Columbidae	3	4	4
Psittacidae	2	1	4
Cuculidae	0	1	1
Caprimulgidae	0	0	1
Trochilidae	5	11	7
Trogonidae	5	1	0
Momotidae	0	1	0
Bucconidae	1	0	0
Galbulidae	1	0	0
Ramphastidae	1	3	0
Picidae	2	4	3
Furnariidae	7	4	2
Dendrocolaptidae	4	4	0
Thamnophilidae	7	1	1
Formicariidae	3	0	0
Rhinocryptidae	1	0	0
Tyrannidae	11	21	12
Cotingidae	1	1	0
Pipridae	1	2	0
Vireonidae	2	4	3
Hirundinidae	0	0	2
Troglodytidae	1	5	3
Sylviidae	1	1	0
Turdidae	0	6	0
Ptilogonatidae	1	0	0
Parulidae	5	13	4
Coerebidae	0	1	0
Thraupidae	5	15	6
Emberizidae	2	3	8
Cardinalidae	0	3	2
Icteridae	1	1	3
Fringillidae	0	0	2

were more likely to be stenophagous than G-species (51.9% of F-species and 27.2% of G-species, $G = 12.15$, df = 1, $P < 0.001$) and F-species were more likely to be strict insectivores than G-species (42.0% of F-species and 21.9% of G-species, $G = 8.87$, df = 1, $P < 0.005$).

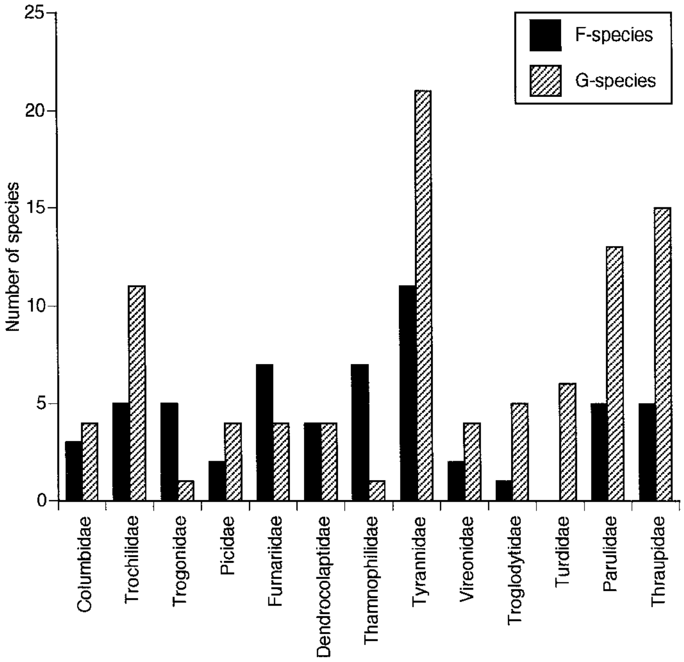


Figure 2. Number of species that were classified as F- or G-species for the 13 families with the most species detected (six or more species per family).

Table 4. Stepwise selection of variables for logistic regression model.

Variable	−2 Log likelihood	Likelihood ratio χ^2-value and p-value[a]	Percent concordance[b]
FORINT	249.544	–	17
STENOPHA	239.842	$\chi^2 = 9.702$, $p < 0.005$	47
SQRTELEV	234.641	$\chi^2 = 5.201$, $p < 0.025$	70

[a] The likelihood ratio shows whether a particular variable added to the model is a significant contribution to the model. For example, adding the variable SQRTELEV to a model containing the variables FORINT and STENOPHA is supported based on the likelihood ratio values.

[b] Each logistic regression model generates a prediction for any particular pair of F- and G-species as to which species is more likely to be the G-species. If the prediction matches the actual observation, this is a concordant result. Percent concordance is based on all possible pairs of F- and G-species. Although FORINT was the first variable selected to enter the model, a model with only FORINT shows a very low concordance because this is a categorical variable and many of the F- and G-species pairs showed the same value for this variable. Hence the model would be unable to determine which species would be more likely to be the G-species. The model with all three of the variables shows a much higher concordance.

In our initial model-building attempt, AIC and likelihood ratio tests showed that elevation was an important variable to include in the model, but models with this variable had poor goodness-of-fit. Hence, we used the transformed variable, square

Table 5. Variables and coefficients selected for the final logistic regression model.

Variable	Estimated coefficient	Standard error	*p*-value	Odds ratio estimate[a]	95% Confidence limits
FORINT	−2.104	0.786	0.007	0.122	0.026–0.569
STENOPHA	−1.078	0.326	0.001	0.340	0.180–0.645
SQRTELEV	0.054	0.024	0.025	1.056	1.007–1.107

[a] Odds ratios are measures of association between two variables, in this case between each predictor variable and the response variable, the likelihood of being a G-species. The odds ratio for FORINT indicates that a change from being a species that uses forest edge/canopy to one that uses only forest interior results in the odds of being a G-species changing to only 12.2% as great as they were. Because SQRTELEV is a continuous variable, the odds ratio estimate indicates that the odds of being a G-species increase 5.6% for each unit increase in SQRTELEV.

root of elevation, in our subsequent model-building. Our final model that best described the probability of being a G-species included the variables FORINT, STENOPHA, and SQRTELEV. This model was also selected by the stepwise logistic regression procedure (SAS 2001; Tables 4 and 5). No interactions between variables were useful additions to the models. The model including these three variables did not show evidence of a poor fit to the data (Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 14.61$, df $= 8$, $P > 0.05$).

Predicted values of the probability of being a G-species were generated for each species using the final model and the data. The quintile (39 species) with the lowest predicted values and the quintile (39 species) with the highest predicted values are in Table 6. Nineteen families are represented in the lowest quintile and 15 families are represented in the highest quintile. Three species of woodcreepers (dendrolocaptids), the three formicariid species detected during the study, and six of the eight thamnophilids detected are in the lowest quintile. Three wrens are also in this quintile, although two are actually G-species. No species from these four families are in the highest quintile. Six hummingbirds (trochilids), six tanagers, and five thrushes are in the highest quintile while no hummingbirds or thrushes and only one tanager is in the lowest quintile. Numbers of warbler and flycatcher (tyrannid) species are approximately equivalent between these two quintiles, with four warblers and eight flycatchers in the highest quintile and three warblers and six flycatchers in the lowest quintile. Of the 39 species with the lowest probability of being G-species, eight were documented as G-species. Of the 39 species in the highest quintile, 29 were G-species.

After finding that the antbirds had the highest proportion of F-species (10/12, 0.83) and the thrushes had the highest proportion of G-species (6/6, 1.00) we conducted *post hoc* tests to compare the elevational ranges of these groups to those of other F- and G-species. The antbirds (Thamnophilidae and Formicariidae) had a significantly lower elevational range than all other F-species (average antbird range $= 1633 \pm 393$ m versus 2029 ± 647 m, $t = 2.05$, $P < 0.05$, $n = 83$) while the thrushes had a significantly higher elevational range than all other G-species (average thrush range $= 2725 \pm 286$ m versus 2140 ± 587, $t = -2.42$, $P < 0.01$, $n = 114$; Appendix).

Table 6. The species predicted to be least likely (20% of all species with the lowest *P*-hat values) and most likely (20% of all species with the highest *P*-hat values) to be able to use agricultural land, based on the logistic regression model.

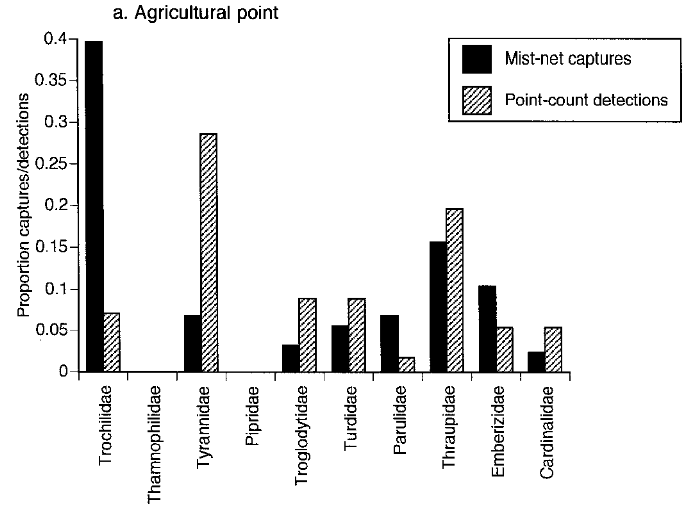
Scientific name	Family	F- or G-status	*P*-hat[a]	Lower confidence limit	Upper confidence limit
Least likely to be G-species					
Lanio leucothorax	Thraupidae	F	0.038	0.007	0.187
Platyrinchus coronatus	Tyrannidae	F	0.053	0.011	0.224
Hylopezus perspicillatus	Formicariidae	F	0.055	0.011	0.230
Grallaricula flavirostris	Formicariidae	F	0.074	0.016	0.279
Microcerculus marginatus	Troglodytidae	G	0.074	0.016	0.279
Platyrinchus mystaceus	Tyrannidae	F	0.088	0.020	0.317
Formicarius analis	Formicariidae	F	0.091	0.020	0.324
Sclerurus mexicanus	Furnariidae	F	0.098	0.022	0.344
Crax rubra	Cracidae	F	0.171	0.042	0.492
Hylophilus ochraceiceps	Vireonidae	F	0.171	0.042	0.492
Tinamus major	Tinamidae	F	0.191	0.048	0.523
Schiffornis turdinus	Tyrannidae	F	0.191	0.048	0.523
Odontophorus guttatus	Odontophoridae	F	0.243	0.064	0.602
Buarremon brunneinucha	Emberizidae	G	0.297	0.078	0.677
Thamnophilus bridgesi	Thamnophilidae	F	0.307	0.170	0.490
Thryothorus semibadius	Troglodytidae	F	0.315	0.179	0.493
Myiobius sulphureipygius	Tyrannidae	F	0.315	0.179	0.493
Terenotriccus erythrurus	Tyrannidae	F	0.315	0.179	0.493
Galbula ruficauda	Galbulidae	F	0.333	0.199	0.500
Microrhopias quixensis	Thamnophilidae	F	0.340	0.208	0.503
Columba speciosa	Columbidae	G	0.348	0.218	0.507
Anabacerthia variegaticeps	Furnariidae	F	0.348	0.218	0.507
Piculus simplex	Picidae	F	0.348	0.218	0.507
Dendrocincla homochroa	Dendrocolaptidae	F	0.365	0.237	0.515
Glyphorhynchus spirurus	Dendrocolaptidae	F	0.365	0.237	0.515
Phaeothlypis fulvicauda	Parulidae	G	0.365	0.237	0.515
Ramphocaenus melanurus	Sylviidae	F	0.365	0.237	0.515
Lepidocolaptes souleyetii	Dendrocolaptidae	G	0.381	0.256	0.524
Chiroxiphia lanceolata	Pipridae	F	0.389	0.265	0.528
Basileuterus tristriatus	Parulidae	F	0.396	0.274	0.533
Thamnistes anabatinus	Thamnophilidae	G	0.396	0.274	0.533
Gymnopithys leucaspis	Thamnophilidae	F	0.396	0.274	0.533
Haplospiza rustica	Emberizidae	F	0.412	0.292	0.543
Cercomacra tyrannina	Thamnophilidae	F	0.412	0.292	0.543
Dysithamnus mentalis	Thamnophilidae	F	0.412	0.292	0.543
Cotinga ridgwayi	Cotingidae	G	0.420	0.301	0.549
Oporornis formosus	Parulidae	F	0.420	0.301	0.549
Henicorhina leucosticta	Troglodytidae	G	0.420	0.301	0.549
Phyllomyias burmeisteri	Tyrannidae	F	0.420	0.301	0.549
Most likely to be G-species					
Campylopterus hemileucurus	Trochilidae	G	0.746	0.650	0.823
Colibri thalassinus	Trochilidae	F	0.746	0.650	0.823
Geotrygon chiriquensis	Columbidae	F	0.756	0.656	0.835

Table 6. (continued)

Scientific name	Family	F- or G-status	*P*-hat[a]	Lower confidence limit	Upper confidence limit
Piaya cayana	Cuculidae	G	0.756	0.656	0.835
Campephilus guatemalensis	Picidae	F	0.756	0.656	0.835
Chlorospingus ophthalmicus	Thraupidae	G	0.756	0.656	0.835
Piranga leucoptera	Thraupidae	G	0.756	0.656	0.835
P. rubra	Thraupidae	G	0.756	0.656	0.835
Amazilia tzacatl	Trochilidae	G	0.756	0.656	0.835
Phaethornis guy	Trochilidae	G	0.756	0.656	0.835
Turdus grayi	Turdidae	G	0.756	0.656	0.835
Attila spadiceus	Tyrannidae	G	0.756	0.656	0.835
Tityra semifasciata	Tyrannidae	G	0.756	0.656	0.835
Micrastur ruficollis	Falconidae	G	0.766	0.662	0.846
Parula pitiayumi	Parulidae	G	0.766	0.662	0.846
Thraupis palmarum	Thraupidae	G	0.766	0.662	0.846
Turdus plebejus	Turdidae	G	0.766	0.662	0.846
Trogon collaris	Trogonidae	F	0.771	0.665	0.851
Saltator striatipectus	Cardinalidae	G	0.776	0.667	0.857
Elaenia frantzii	Tyrannidae	G	0.776	0.667	0.857
Icterus galbula	Icteridae	G	0.784	0.671	0.866
Basileuterus rufifrons	Parulidae	G	0.784	0.671	0.866
Lampornis castaneoventris	Trochilidae	G	0.789	0.674	0.871
Bolborhynchus lineola	Psittacidae	F	0.793	0.676	0.876
Catharus aurantiirostris	Turdidae	G	0.793	0.676	0.876
C. ustulatus	Turdidae	G	0.793	0.676	0.876
Vermivora peregrina	Parulidae	G	0.801	0.679	0.884
Aulacorhynchus prasinus	Ramphastidae	G	0.801	0.679	0.884
Piranga flava	Thraupidae	F	0.801	0.679	0.884
Zimmerius vilissimus	Tyrannidae	G	0.801	0.679	0.884
Mionectes olivaceus	Tyrannidae	F	0.801	0.679	0.884
Pachyramphus versicolor	Tyrannidae	F	0.801	0.679	0.884
Turdus assimilis	Turdidae	G	0.809	0.682	0.893
Elanoides forficatus	Accipitridae	F	0.823	0.688	0.907
Colibri delphinae	Trochilidae	F	0.826	0.689	0.911
Myiarchus tuberculifer	Tyrannidae	G	0.830	0.691	0.914
Oporornis philadelphia	Parulidae	G	0.928	0.704	0.986
Ramphocelus costaricensis	Thraupidae	G	0.941	0.752	0.988
Tyrannus melancholicus	Tyrannidae	G	0.966	0.843	0.993

[a] *P*-hat is the predicted probability that a species is a G-species, that is, detected in both forest and agricultural land covers.

Distributions of the numbers of individuals per family detected through netting or point counts were significantly different for five of the seven points where both techniques were used (Kolmogorov–Smirnov two-sample tests, $P < 0.05$ for five of seven points, using the sequential Bonferroni technique). Hummingbirds and manakins (piprids) were more likely to be detected (and identified) with mist nets than with point counts. Hummingbird captures made up 27.9% of all mist-net



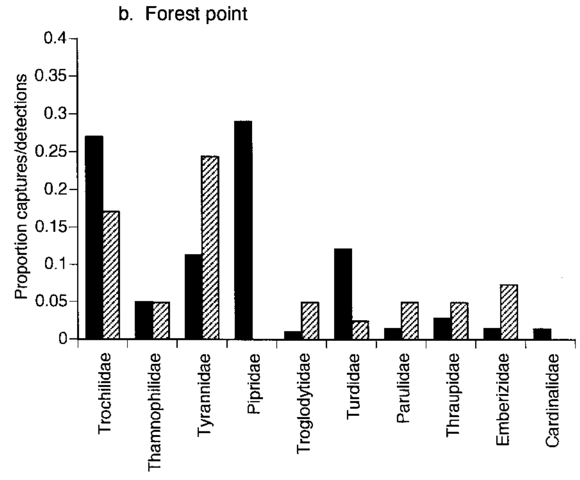


Figure 3. Proportions of total individuals captured in mist nets or detected by point counts at one agricultural point and one forest point where both techniques were used. Graphs show data for only the 10 most commonly detected families.

captures at the seven points and manakins made up 6.9% of the total, while hummingbirds were only 6.2% and manakins 0% of the total point-count detections at the seven points. Flycatchers, in contrast, were more likely to be detected with point counts than with mist nets, with 9.1% of all mist-net captures being flycatchers and 19.9% of all point-count detections being flycatchers. Distributions of point-count and mist-net detections for the 10 most commonly detected families for two of the sampling points are shown in Figure 3.

Discussion

Model results

Although the univariate analyses revealed a number of potential associations between the predictor variables and the probability of being a G-species, some of the predictor variables were associated with each other. For example, of the 73 species that were stenophagous, 59 were insectivores. Hence the logistic regression technique provided us with a more robust manner of detecting relationships between particular traits and the likelihood of being a G-species, because two variables that were highly correlated would not both show up as important predictors.

According to the logistic regression model, the dependence of a species on forest interior was inversely related to the probability of being a G-species. Forest species exhibit a diversity of habitat affinities, using various combinations of forest edge, canopy, and interior habitats (Stiles 1983; Stouffer and Bierregaard 1995; Restrepo et al. 1999). The edge/canopy habitats have vegetation–air interfaces, as do agricultural land covers, which may predispose species that use these habitats to use agricultural land covers (Stiles 1980). This type of species distribution pattern, with forest canopy species more often detected in agricultural land covers than forest interior species, was evident in Amazonian Peru (Terborgh and Weske 1969). Species using edge/canopy habitats in forest are more likely to enter gaps in forest cover than interior species (Sieving et al. 1996; Desrochers and Hannon 1997; St. Clair et al. 1998), which may facilitate their movement into agricultural land covers. Many of the tanagers and hummingbirds, among the most common of our G-species, have these edge and/or canopy affinities while the great majority of antbirds of the families Formicariidae and Thamnophilidae (10 of 12) and some of the woodcreepers (4 of 8), many of which are associated with forest interior, were F-species.

Diet and/or foraging behavior specialization have been cited and documented as risk factors that may prevent tropical forest birds from using agricultural lands (Terborgh and Weske 1969; Thiollay 1995) and from maintaining populations in forest fragments (Wilson and Willis 1975; Stouffer and Bierregaard 1995). Our model results support the idea that stenophagous forest dwellers are less likely to be able to successfully forage in novel agricultural habitat types than species with broader diets. Although we found no additional predictive value if the variable INSECT was added to the model, the majority of stenophagous species were insectivores. Hence, diet breadth and insectivory are associated and the relationship between insectivory and a forest species' ability to use agricultural land covers bears further investigation.

We used elevational range as a surrogate for the tolerance of a species to environmental conditions and found that species with broader elevational ranges were more likely to be G-species. This finding supports the idea that forest specialists may be less able to cope with disturbances that result in fluctuating conditions than forest generalists. Although tropical forests experience some disturbance from tree falls caused by storms, landslides, and other phenomena (Hartshorn 1980), agricultural land covers like pastures and coffee plantations are both more frequently disturbed per unit area, for example, by cutting and mowing, and are more adverse environments for forest-dwelling organisms than the tropical forest they replace. For example, sun coffee plantations lack critical resources like protection from the elements (Roberts et al. 2000) and pastures have microclimates with lower moisture availability (Nepstad et al. 1991), and higher air and soil temperatures (Holl 1999) than forest. Agricultural land covers are also expected to show greater variability than forest in daily temperature and moisture conditions (Salati and Nobre 1991). Hence, forest species with broader environmental tolerances are more likely to be able to inhabit both tropical forest and agricultural land covers than species with narrower tolerances.

Elevational range is a crude measure of a species' environmental tolerance and elevational data are sparse for many species (Stotz et al. 1996). However, our results, showing that the most forest-restricted families, the Thamnophilidae and the Formicariidae, have an even narrower mean elevational range than the other F-species while the least forest-restricted family, the Turdidae, has a greater mean elevational range than the other G-species, indicate that it is a useful character in identifying forest species at risk from deforestation. This may be particularly true in countries like Costa Rica with a large range of elevations (Gillespie 2001).

Taxonomy of F- and G-species

The model results suggest mechanisms to explain some of the taxonomic patterns documented here and in other work, for example, the finding that some groups, particularly the antbirds, are unlikely to use agricultural and early second-growth land covers in the Neotropics (Terborgh and Weske 1969; Johns 1991; Robbins et al. 1995). The antbirds generally use forest interior, are stenophagous, and have relatively narrow elevational ranges. In contrast, all six thrush species were G-species and the thrushes use forest edge and canopy, have diverse diets, and relatively wide elevational ranges.

Some of the taxonomic patterns did not reflect the model predictions. For example, five of six trogon species were F-species and 80 of 81 trogon point-count detections were in forest, despite their affinities for forest edge and canopy and their generally diverse diets. In fact, the predicted values generated from the model for the six trogon species are all greater than 0.5, making them more likely to be G-species than F-species. This discrepancy between model predictions and reality may be due to the lack of large trees in many of the simplified agricultural areas, limiting the perches available to trogons. Also, agricultural microclimates and vegetation structure may not allow the existence of their preferred fruits, large insects, and small vertebrates. However explained, these apparent contradictions suggest some of the limitations of the model.

First, we did not examine a number of other traits such as lifespan, fecundity, and nest type that may vary between forest species that are and are not able to use agricultural land covers (Greenslade 1983; Ford et al. 2001). Information on these traits is lacking for many tropical bird species. For example, 8.7% of the F- and G-species we detected have not even had their nests officially described (Stiles and Skutch 1989). The information we were able to find on basic natural history characteristics such as diet and weight were from compilations of data based on numerous intense and lengthy investigations (Stiles and Skutch 1989; Karr et al. 1990; Stotz et al. 1996). These types of detailed data, with a future focus on demographic characteristics, will be crucial in efforts to further our abilities to predict which species will decline and which will be able to withstand continued anthropogenic changes in tropical landscapes.

Second, as demonstrated from our net and point-count data, different sampling techniques detect particular types of species more or less frequently, supporting the use of multiple sampling techniques to most accurately characterize the distributions of species across different land cover types (Blake and Loiselle 2001). Since the majority of our data were collected by point counts, we expect that our results concerning the classification of F- and G-species are stronger for those species that are more easily detected by point counts rather than mist nets.

Third, our classification of rare species as F- or G-species may be problematic in some cases. For example, we detected the slaty finch, *Haplospiza rustica*, one time through netting in mature forest and so it was classified as an F-species. However, Stiles and Skutch (1989) describe the species as primarily one of pastures, clearings, and second growth. Hence, our classifications of rare species or those not easily detected by mist nets or point counts are likely less secure than those for species commonly detected.

Despite these limitations, this exploratory analysis has provided insight into the types of characteristics that predispose forest species to be able to use agricultural lands. Recent work suggests that the ability to use deforested land is a key determinant of a species' ability to persist in forest fragments (Sekercioglu et al. 2002). Hence, development of our capacity to predict which forest species can use agricultural land will assist in determining which species are and are not likely to survive forest conversion and fragmentation.

Comparisons with other regions

In comparison with some of the agricultural land covers in other parts of Latin America, those of our study region appear less able to support a number of forest species. The proportions of F- and G-species we detected were different than those reported in a study that compared bird species richness in forest and agricultural land covers in Los Tuxtlas, Mexico (Estrada et al. 1997). F-species made up only 16.4% of the species detected in the Mexico study, compared to our 29.9%, and G-species comprised 62.4% versus our 42.1%. This difference likely results from a difference in the types of agricultural systems sampled in the two study sites. The coffee plantations sampled by Estrada and colleagues had tall (>15 m) forest trees while the coffee plantations our routes traversed in Costa Rica did not have such trees but instead had banana plants, short stature (3–7 m) legumes, or no plants besides coffee. Hence, some of the agricultural land covers sampled in Mexico apparently provided habitat for forest species that was unavailable in the majority of agricultural land covers sampled in Costa Rica, leading to more G-species at the Mexico site. For example, we detected the wedge-billed woodcreeper only in forest while Estrada and colleagues detected it in both forest and coffee land covers. Similarly, nine other species that we detected only in forest (collared trogon, violaceous trogon, pale-billed woodpecker, spot-crowned woodcreeper, black-faced antthrush, tufted flycatcher, black-throated green warbler, Kentucky warbler, and red-crowned ant-tanager) were detected in coffee plantations in Chiapas, Mexico by Greenberg et al. (1997b). Some of the coffee plantations sampled by Greenberg et al. (1997b) were structurally simpler than traditional forest-like plantations but commonly had trees from 8–12 m in height and hence had more foliage-height diversity than the Costa Rican plantations our sampling routes traversed. These comparisons indicate that the simplified agricultural systems currently dominating our study region do not provide habitat for some forest species which are able to use different types of agricultural systems in other regions.

We suggest that our results represent a best-case scenario in terms of the types of species the agricultural land covers in our study region may support, because the presence of a species does not ensure that the species will be able to successfully reproduce in such a land cover. In addition, species that appear to be flexible in land-cover use in that we detected them along both forest and agricultural routes, for example, the white-throated robin, *Turdus assimilis*, may be dependent on forest for some life stages (Cohen and Lindell, in press) and so would not survive in an agricultural landscape devoid of forest. The types of agricultural systems that dominate much of Coto Brus are inhospitable to nearly a third of the species we detected in this study. Hence, continued conversion of forest to agriculture is likely to result in virtually complete habitat loss for much of the regional avifauna. We suggest that this likelihood underscores the importance of maintaining the forested protected areas within the region, including the Amistad Biosphere Reserve.

Acknowledgements

We appreciate the willingness of the following landowners to let us work on their property: Roig Mora, Addison Fischer, Roberto Montero, Julio Gonzalez, Roy Chavez, and Norman Gonzalez. We thank Luis Diego Gómez for his support of our work at the Las Cruces Forest Reserve and the Las Alturas Biological Station and Fernando Castañeda for support at Las Alturas. Glen Adelson, Jeffrey Brawn, and an anonymous reviewer provided useful comments on earlier versions of the manuscript. Financial support was provided by several administrative units at Michigan State University and NASA's Interdisciplinary Science Program. We appreciate the field assistance of Diane Cox, Daniel Holley, John Lindell, Mary Marquis, Mike Roberts, Randi Sandí, and Ronald Soto.

Appendix

F-species and associated characteristics.

Scientific name	Family	Forest interior dependence[a]	Stenophagous[b]	Elevational range (m)
Tinamus major	Tinamidae	2	0	1700
Elanoides forficatus	Accipitridae	1	0	3300
Accipiter bicolor	Accipitridae	1	1	2700
Spizaetus ornatus	Accipitridae	1	1	3000
Crax rubra	Cracidae	2	0	1500
Chamaepetes unicolor	Cracidae	1	1	2500
Odontophorus guttatus	Odontophoridae	2	0	2200
Eurypyga helias	Eurypygidae	1	0	1800
Geotrygon chiriquensis	Columbidae	1	0	2500
Leptotila cassinii	Columbidae	1	0	1400
Geotrygon montana	Columbidae	1	1	2600
Bolborhynchus lineola	Psittacidae	1	0	2900
Pyrrhura hoffmanni	Psittacidae	1	1	3000
Colibri delphinae	Trochilidae	1	0	3350
C. thalassinus	Trochilidae	1	0	2400
Eupherusa eximia	Trochilidae	1	0	2150
Heliodoxa jacula	Trochilidae	1	0	2150
Thalurania colombica	Trochilidae	1	0	1900
Trogon bairdii	Trogonidae	1	0	1250
T. collaris	Trogonidae	1	0	2650
T. massena	Trogonidae	1	0	1200
T. rufus	Trogonidae	1	0	1400
T. violaceus	Trogonidae	1	0	1850
Malacoptila panamensis	Bucconidae	1	0	1250
Galbula ruficauda	Galbulidae	1	1	1300
Eubucco bourcierii	Ramphastidae	1	0	2000
Campephilus guatemalensis	Picidae	1	0	2500
Piculus simplex	Picidae	1	1	1400
Hyloctistes subulatus	Furnariidae	1	0	1700
Syndactyla subalaris	Furnariidae	1	0	2200
Anabacerthia variegaticeps	Furnariidae	1	1	1400
Philydor rufus	Furnariidae	1	1	2200
Sclerurus mexicanus	Furnariidae	2	1	2200
Xenops minutus	Furnariidae	1	1	2200
X. rutilans	Furnariidae	1	1	2800
Campylorhamphus pusillus	Dendrocolaptidae	1	1	2200
Dendrocincla homochroa	Dendrocolaptidae	1	1	1500
Glyphorhynchus spirurus	Dendrocolaptidae	1	1	1500
Lepidocolaptes affinis	Dendrocolaptidae	1	1	3050
Myrmeciza exsul	Thamnophilidae	1	0	900
Cercomacra tyrannina	Thamnophilidae	1	1	1800
Dysithamnus mentalis	Thamnophilidae	1	1	1800
Gymnopithys leucaspis	Thamnophilidae	1	1	1700
Microrhopias quixensis	Thamnophilidae	1	1	1350
Myrmotherula schisticolor	Thamnophilidae	1	1	2200

Appendix (continued)

Scientific name	Family	Forest interior dependence[a]	Stenophagous[b]	Elevational range (m)
Thamnophilus bridgesi	Thamnophilidae	1	1	1150
Formicarius analis	Formicariidae	2	1	2050
Grallaricula flavirostris	Formicariidae	2	1	1700
Hylopezus perspicillatus	Formicariidae	2	1	1250
Scytalopus argentifrons	Rhinocryptidae	1	1	2100
Mionectes olivaceus	Tyrannidae	1	0	3000
Ornithion semiflavum	Tyrannidae	1	0	1250
Pachyramphus versicolor	Tyrannidae	1	0	3000
Rhytipterna holerythra	Tyrannidae	1	0	1200
Schiffornis turdinus	Tyrannidae	2	0	1700
Mitrephanes phaeocercus	Tyrannidae	1	1	3500
Myiobius sulphureipygius	Tyrannidae	1	1	1200
Phyllomyias burmeisteri	Tyrannidae	1	1	1850
Platyrinchus coronatus	Tyrannidae	2	1	1200
Platyrinchus mystaceus	Tyrannidae	2	1	2000
Terenotriccus erythrurus	Tyrannidae	1	1	1200
Procnias tricarunculata	Cotingidae	1	1	2400
Chiroxiphia lanceolata	Pipridae	1	1	1650
Hylophilus ochraceiceps	Vireonidae	2	0	1500
Vireolanius pulchellus	Vireonidae	1	0	1800
Thryothorus semibadius	Troglodytidae	1	1	1200
Ramphocaenus melanurus	Sylviidae	1	1	1500
Ptilogonys caudatus	Ptilogonatidae	1	0	1800
Basileuterus culicivorus	Parulidae	1	0	2100
B. tristriatus	Parulidae	1	1	1700
Dendroica virens	Parulidae	1	1	3000
Oporornis formosus	Parulidae	1	1	1850
Seiurus motacilla	Parulidae	1	1	2600
Euphonia imitans	Thraupidae	1	0	1400
Habia rubica	Thraupidae	1	0	2250
Piranga flava	Thraupidae	1	0	3000
Tachyphonus luctuosus	Thraupidae	1	0	2200
Lanio leucothorax	Thraupidae	2	1	800
Arremon aurantiirostris	Emberizidae	1	0	1200
Haplospiza rustica	Emberizidae	1	1	1800
Cacicus uropygialis	Icteridae	1	0	2300

[a] 0 = dependent on non-forest habitats and not using forest edge and/or canopy, 1 = using forest habitats including forest edge and/or canopy, and 2 = dependent on forest interior and not using forest edge and/or canopy.

[b] 0 = eating more than one food type and 1 = eating only one food type.

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