REPORT

Conservation of tropical forest birds in countryside habitats

Jennifer B. Hughes,*
Gretchen C. Daily and Paul R. Ehrlich
Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, U.S.A.
**Correspondence and present address: Department of Ecology and Evolutionary Biology and Center for Environmental Studies, Brown University, Providence, RI 02912, U.S.A.*
Tel.: +1 (401) 863-9676.
Fax: +1 (401) 863-2166.

Abstract

The pressing need to increase agricultural production often seems at odds with conserving biodiversity. We find that if managed properly, the tropical countryside may provide a substantial opportunity for tropical bird conservation. We detected 144 bird species from 29 families in agricultural areas outside of extensive native forest in southern Costa Rica. The majority of the species detected were observed foraging, often kilometres from extensive native forest. We estimate that 46% of those native to this region (excluding nocturnal species and waterfowl) are utilizing the countryside in some manner. Forecasts of biodiversity change under various land-use scenarios indicate that policies that affect habitat composition could greatly impact the persistence of these species in the countryside. In particular, if tall trees and edge habitats were removed from this landscape, we predict that bird richness in the countryside would decline by approximately 40%.

Keywords

Biodiversity, extinction rates, matrix, Costa Rica.

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INTRODUCTION

Historically, ecologists have assumed that few tropical forest animals and plants survive in agricultural landscapes. This assumption is implicit in most forecasts of extinction rates, which are typically based on species–area relations and rates of destruction of tropical forest (e.g. Lawton & May 1995). Yet deforested countryside may retain substantial 'forest' biodiversity, especially in landscapes with a variety of land uses (Robbins *et al.* 1992; Toledo *et al.* 1994; Petit *et al.* 1995; Greenberg *et al.* 1997b; Medellín *et al.* 2000). Even in temperate countrysides such as Europe where most forest was converted to agriculture centuries ago, a substantial fraction of diversity is retained (Duelli *et al.* 1990; Pain *et al.* 1997; Pärt & Söderström 1999; Chamberlain *et al.* 2000), and efforts are underway to restore a richer biota (e.g. RSPB 2001).

Recent limited surveys in open tropical countryside of the Las Cruces region of Costa Rica – largely deforested in the past half-century – detected 62% of fruit-feeding butterflies, 42% of forest-trapped moth morphospecies, and 65% of non-flying mammal species. Many more native species occur in scattered 0.1–30-ha remnants of forest (G. Daily unpublished data; Daily *et al.* 2001; Ricketts *et al.* 2001). Here we report patterns of habitat and resource use by birds in habitats of the Las Cruces countryside. Based on these habitat associations, we then forecast how bird diversity in the countryside might change under likely scenarios of future land use. These scenarios suggest that relatively minor changes in land use may have a major impact on the local bird diversity.

METHODS

We surveyed 53 randomly chosen sites within a 15-km radius of the Organization for Tropical Studies' Las Cruces field station, Coto Brus, Costa Rica. Today, the Las Cruces region is largely deforested and comprises a mosaic of countryside habitats: cattle pastures, coffee plots, mixed agricultural plots, gardens, thin riparian strips of native vegetation and small forest remnants. The 227-ha Las Cruces Reserve adjacent to the station is the largest remnant of mid-elevation forest in the region. The other large tracts of forest are along ridge lines higher in elevation or in relatively thin, linear stretches, often along streams.

The surveys took place between 26 January and 10 March 1998. Our goal was to sample habitats in proportion to their occurrence in the countryside; therefore, we chose the sites at random from a map of the very extensive network of small (mostly unpaved) roads. Most sites were more than 1 km from other sites (three sites were only 0.5–1 km apart). We did not sample in heavily forested areas, such as the Las Cruces Reserve, or areas without roads. At a site, we walked in a randomly selected direction at a slow pace, stopping only to record new individuals; we continually moved through new areas to avoid double-counting individuals. Two to three people surveyed each site between 0545 h and 0915 h for a total of 330 person-hours and an average of 6.0 person-hours per site. We focused on the individuals that we saw, but if we heard a bird that we could not identify, we would sometimes record and playback the call until we observed the individual. We did not walk inside of forest fragments, but we recorded species that we saw on the edges of fragments.

To determine the bird communities associated with different countryside habitats, we recorded the habitat in which each bird was observed during our surveys. Habitats were classified as either 'plots' or 'edges.' Plots were areas used for food or timber production and included active pasture, fallow fields and plantations of coffee, yucca, shade coffee and pine. Edges were vegetation that bordered plots, roads and homes, and were divided into eight types: ground (including low herbs) and 7 possible combinations of tangles, shrubs and trees. We defined shrubs as ornamental plants and single bushes and 'tangle' as vegetation other than shrubs and trees that is > 0.5 m tall (usually a mixture of bushes and vines). Thus, the most vertically complex edge type was a tree–shrub–tangle edge. We included the outside edge of forest remnants (typically < 1 ha) in this edge class.

In addition to recording habitat type, we also recorded the microhabitat in which every individual was found and visually estimated the height of the microhabitat in metres. Finally, we recorded the activity (foraging, nesting, moving only, or perching only) of each bird we observed.

Using the program EstimateS (Colwell 1999), we compared total species richness among the different habitat types using six different estimation methods (the bootstrap, Chao 2, first-order jackknife, second-order jackknife, incidence-coverage and Michaelis-Menten estimators).

To investigate how the number of bird species in the countryside might change under different land-use regimes, we compared estimated richness today to estimated richness under five future scenarios. We used the EstimateS software (Colwell 1999) to calculate a first-order jackknife estimate of total species richness. This estimator estimates total richness from the observed pattern of relative species abundances across different sites. We chose this estimator because it yielded mid-range values in Figs 2 and 3, and because it has performed well in other studies (as cited in Boulinier *et al.* 1998). To estimate species richness in countryside habitats today, we calculated the jackknife estimate with all of our observations. To estimate species richness under each scenario, we simply excluded those observations that occurred in particular habitat types and re-calculated the jackknife estimate. For instance, to estimate total richness in a landscape without tall trees, we excluded all observations of birds in tall trees and recalculated the jackknife estimate with EstimateS.

RESULTS

We recorded 5006 individuals from 144 native species and 29 families (we exclude nocturnal species and waterfowl throughout this paper). These birds include 38% of the species and 64% of the families reported in this region (James Zook, unpublished data). The recorded species were native and not solely open habitat species. Only 49 of the species are thought to be restricted to open habitats; the remaining 66% are found in both forest and open areas (57 species) or are restricted to forest (38 species) (see Appendix). In addition, 18% of the species we observed were long-distance migrants, the same percentage of migrants reported in the region.

Randomly selecting sites appeared to sample habitats in proportion to their occurrence. Based on satellite image classifications, 31% of the non-forested area of this region is pasture and 25% coffee (Sallie-Anne Bailey, unpublished data). In comparison, during our surveys we spent 32% of our time in active pastures and 29% in coffee.

Habitat use

Individuals observed per person-hour differed significantly among the three main plot types: active pasture, fallow fields and coffee plantations ($\chi^2 = 99.320$, d.f. = 2, $P < 0.001$). On average, 4.1 individuals were observed in active pasture per person-hour, in contrast to 9.9 in fallow fields and 7.2 in coffee plantations. Edges make up a small fraction of the landscape area, and thus we were often surveying in the interior of a plot far from edges. Nevertheless, we observed 66.3% of all individuals in edges. The frequency of individuals observed in edges vs. plots varies by family (for families with > 25 individuals observed; $G = 74.90$, d.f. = 17, $P < 0.001$; Fig. 1). A test of homogeneity (Sokal & Rohlf 1995) reveals that more often than average, eight families (Sylviidae to Emberizidae in Fig. 1) were found in plots and 10 families (Thraupidae to Vireonidae in Fig. 1) were found in edges.

To standardize for observation time and estimate the average number of species observed at a site, we used rarefaction curves (Heck *et al.* 1975) (with observation time on the x-axis and species richness observed on the y-axis). For 6.3 person-hours, the average observation time at a site, on average 31 species were observed in fallow fields vs. 18 species in active pastures, and this difference was significant at the 0.05 level (the 95% confidence intervals did not cross). There was no significant difference between

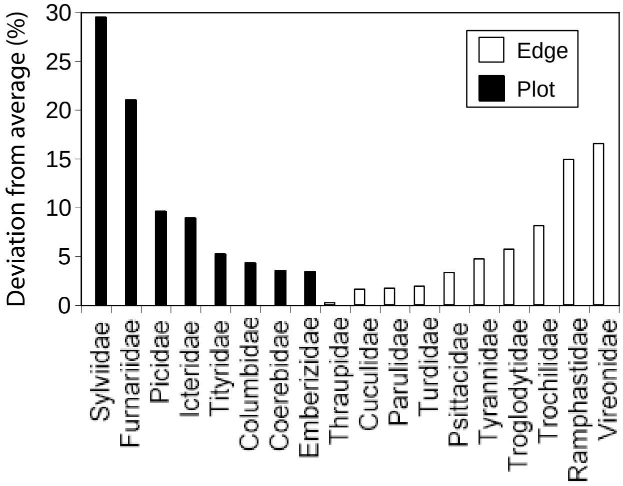

Figure 1 The percentage difference between number of individuals observed in plot or edge habitats within a family and the average across all families. Only the positive deviations are shown; however, every positive deviation signifies an equal negative deviation in the other habitat. On average across all families, 66.3% of individuals were encountered in edges and 33.7% in plots.

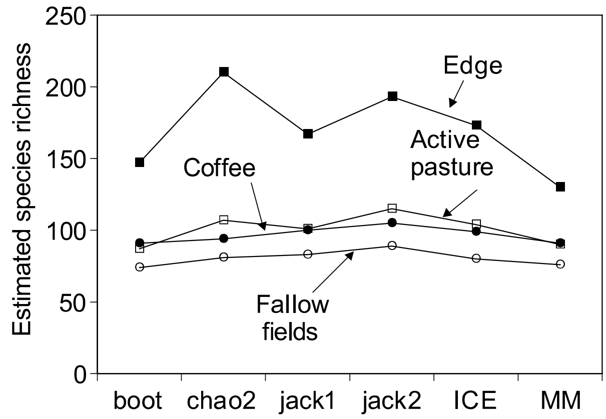

Figure 2 Estimated species richness of the four major countryside habitats for six different estimators (boot: bootstrap, chao2: Chao 2, jack1: first-order jackknife; jack2: second-order jackknife; ICE: Incidence-Coverage Estimator, MM: Michaelis-Menten).

the number of species observed in fallow fields and coffee plots.

All of the six estimators predict that edges are more species-rich than the three main plot types and that among plot types, fallow fields are the least species-rich (Fig. 2). Based on the rarefaction analyses above, however, observed local richness is higher in fallow fields than active pastures. Thus, it appears that there is greater species turnover among active pasture sites than fallow field sites.

Among particular edge types, the most vertically complex edge (tree–tangle–shrub edge) contains the richest bird fauna (Fig. 3). The three other edge types that contain trees rank as the next richest edges, whereas edge types without trees rank as the most depauperate.

Resource use

All of the species that we observed more than 13 times ($n = 60$) were detected foraging. *Coereba flaveola* was observed nesting seven times; *Thraupis episcopus* and *T. palmarum* three times; *Melanerpes rubricapillus*, *Ramphocelus passerinii* and *Turdus grayi* twice; and *Columbina talpacoti*, *Columba speciosa*, *Saltator albicollis* and *Tiaris olivacea* once. The activity of an individual and habitat type (edge or plot) was not independent ($\chi^2 = 17.39$, d.f. $= 3$, $P < 0.001$). More individuals were observed foraging and nesting in edges than expected given the number of individuals observed in edges (Table 1). This result suggests that edges provide better habitat for foraging

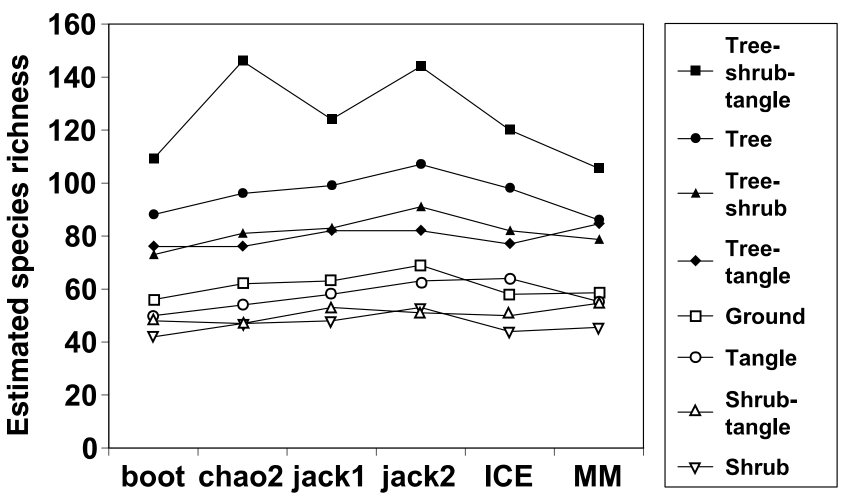

Figure 3 Estimated species richness of the eight edge classes for six different estimators. Filled symbols are edge classes that include trees. Abbreviations as in Fig. 2.

Table 1 The number of individuals observed in edge and plot habitats performing different activities.

	Habitat	
Behaviour	Plot	Edge
Foraging	508	1124
Moving	222	401
Nesting	4	19
Perching	966	1663
Total	1700	3207

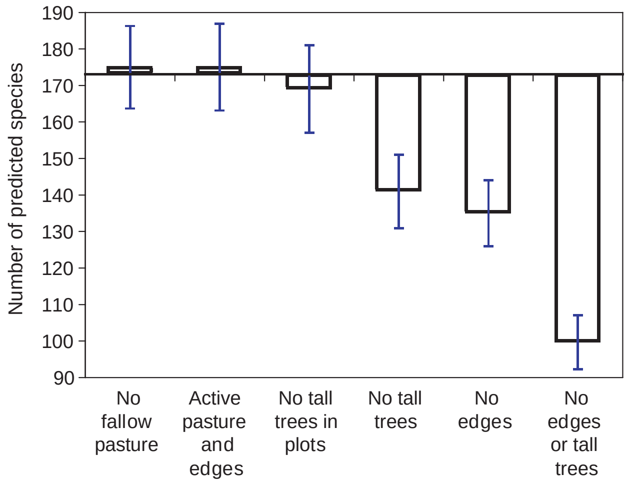

Figure 4 The number of bird species predicted to remain in the countryside under six land-use scenarios. The axis crosses at 173 species, the estimated number of current species (using the first-order jackknife estimator), so that the bar length represents the change in species richness from current richness. Error bars are 95% confidence intervals.

and reproduction than plots. Because only 23 individuals from 10 species were observed nesting, however, data on a broader range of species' nesting habits in the countryside are needed to assess the generality of this result.

Land-use scenarios

With the jackknife estimator, we estimated that 173 bird species currently occur in the countryside, or 46% of the 380 species thought to occur in the area. Thus, it appears that 54% of the native species are restricted completely to forest.

A common outcome of agricultural intensification is a reduction in the variety of plot types and in the amount of fallow land (McNeely & Scherr 2001). In this part of Costa Rica, a likely scenario is conversion of fallow fields or coffee plots to active pasture. In either of these cases, bird richness in the study area is not predicted to change significantly from present richness (Fig. 4).

Another probable scenario is a reduction in the number of tall trees resulting from timber harvesting and poor seedling recruitment in agricultural landscapes (Gascon *et al.* 2000; Laurance *et al.* 2000). If tall trees from the plots were removed (i.e. excluding records of individuals that were observed in trees > 10 m), species richness is not predicted to change significantly; however, if tall trees in both edges and plots are lost, richness is predicted to drop significantly (to 141 species; Fig. 4). Thus, as noted in the analyses above, a large fraction of bird diversity appears dependent on trees in edge habitats (see also, Harvey 2000). If all edges are lost (a likely trend if plot sizes become larger), we predict that species richness will be further reduced (to 135 species; Fig. 4). It is important to emphasize that the results of the land-use scenarios depend on the starting context. For instance, while removing the tall trees in plots from the current landscape may not change bird richness, removing these same trees from a countryside without edges is predicted to reduce bird diversity by 35 additional species (Fig. 4).

DISCUSSION

Although more than half of the bird species in this region appear to be restricted entirely to forest, policies that affect habitat composition in the countryside could help secure the persistence of 173 native species. Thus, while deforested habitats are doubtless not a substitute for extensive forest, our results suggest an opportunity for increasing both local bird diversity and the viability of many species' populations by actively managing the composition of countryside habitats.

Our analyses suggest that, in general, plot composition may not matter to countryside bird diversity as long as thick edges and small forest remnants with tall trees are present. It has long been known that as a general rule, vertical complexity of vegetation is important to bird diversity (MacArthur & MacArthur 1961; Roth 1976), and this rule may hold in human-dominated habitats as well (e.g. Greenberg *et al.* 1997a). One of our results that may at first appear to contradict this conclusion (and other studies, e.g. Saab & Petit 1994) is that active pastures in this region support more species than fallow fields (Fig. 2). Yet within sites, observed bird species richness was on average higher in fallow fields than active pastures. Thus, it appears that there is greater species turnover (beta diversity; Whittaker 1972) between active pastures than fallow fields.

Although we observed only 10 species nesting, for two reasons we propose that many more species are actually breeding in the countryside. First, our surveys were done outside of peak breeding season; most resident species reproduce between April and June (Slud 1976; Stiles & Skutch 1989). Second, we observed forest birds foraging extensively in sites far from large tracts of forest. The mean minimum distance of our sites to large forest (≥ 200 ha) is 2.6 km (SD ± 1.7). While little is known about the distribution of home ranges of birds in this area, studies of birds from other parts of the world indicate that most species have home ranges between one and a few hundred hectares (Okia 1976; Terborgh *et al.* 1990; Baillon *et al.* 1992; Freemark *et al.* 1995). Thus, it seems unlikely that most birds would travel more than 2 km from nesting areas in the forest to forage on a daily basis. Seasonal migrations within this landscape may, however, be a factor if some species move closer to forest during the breeding season (Hilty 1994). We also surveyed nearby palm plantations (elevation 50 m, near the city of Neily, Puntarenas) where palm monocultures are grown in plots without hedgerows and are more that 6 km from extensive forest. In only 23 person-hours, we observed 43 native species, indicating again that some native species are indeed capable of surviving, if not reproducing, in human-dominated areas far from forest.

Even if many bird species are reproducing in the countryside, in the absence of detailed population studies on every species we cannot say whether these populations are sustainable, i.e. whether they are source or sink populations (Pulliam 1988) and thus whether countryside bird diversity is in decline. Brooks *et al.* (1999) show that in tropical forest fragments bird diversity may still be declining 50 years after isolation, but the time scale of relaxation in countryside habitats is unknown. Similarly, our data do not indicate whether a particular species can survive solely within a habitat in which it is detected. Finally, many factors other than habitat loss will affect the persistence of bird species in agricultural areas, including habitat geometry (Freemark *et al.* 1995), predation (Gates & Gysel 1978; Bayne & Hobson 1997) and farming practices, such as pesticide and herbicide applications (Campbell *et al.* 1997; Boutin *et al.* 1999). Thus, our scenarios probably overestimate the bird diversity that will be able to survive in the long term.

We argue, however, that these limitations should not prevent us from making rough estimates of biodiversity loss, because only in this manner can we weigh the consequences of alternative land-use policies for biodiversity (see, e.g. Sala *et al.* 2000). The simple analysis here demonstrates that the total amount of bird diversity supported in the countryside may be substantially enhanced by appropriate land-use decisions. Our study also points to ecological and evolutionary questions for future study in human-dominated landscapes, concerning the ecological roles that surviving species will play and the influence of human-induced extinctions on the future course of evolution (e.g. Daily 2001; Myers & Knoll 2001).

The benefits of maintaining populations of native bird species in the countryside are twofold. First, this diversity is likely to supply valuable ecosystem services for humanity's sake, including aesthetic values, pollination, pest control and seed dispersal for the maintenance of vegetation cover and its associated benefits (Daily 1997; Balvanera *et al.* 2001). Second, while for many species there will be no substitute for extensive native habitats, the tropical countryside may provide substantial conservation opportunities for biodiversity's sake. This window of opportunity will close soon as pressures to increase food production intensify, unless biodiversity conservation is integrated explicitly into agricultural policy.

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APPENDIX

Native bird species detected during the surveys, their habitat affiliation, and the number of individuals detected in each habitat type.

Family	Species	Habitat affiliation*	Edge	Plot type: Active pasture	Coffee	Fallow fields	Other†	Total individuals
Accipitridae	*Buteo magnirostris*	O	2				2	4
	Buteo platypterus	O	1		2			3
	Elanoides forficatus	B	1	2	1			4
Cathartidae	*Coragyps atratus*	B	6				0	6
Coerebidae	*Coereba flaveola*	B	54	6	15	11	1	87
Columbidae	*Claravis pretiosa*	O		2				2
	Columba cayennensis	B		1				1
	Columba nigrirostris	F	7			2		9
	Columba speciosa	B	11	4	4	9		28
	Columbina talpacoti	O	54	2	6	14		76
	Leptotila verreauxi	B	21	5	5	3	2	36
Cracidae	*Ortalis cinereiceps*	B				2		2
Cuculidae	*Crotophaga ani*	O	43	7		2		52
	Piaya cayana	B	10	3	5	7	2	27
	Tapera naevia	O		1			9	10
Dendrocolaptidae	*Campylorhamphus pusillus*	F	1					1
	Lepidocolaptes souleyetti	B	6		1			7
	Woodcreeper sp.	–	3					3
	Xiphorhynchus guttatus	F	1					1
Emberizidae	*Arremonops conirostris*	O	77	6	11	19	3	116
	Oryzoborus funereus	O	1			1		2
	Pheucticus ludovicianus	O	18	1			1	20
	Saltator albicollis	O	43	1	12	11	1	68
	Saltator maximus	B	81	5	18	17	1	122
	Sphorophila aurita	O	75	10	34	15	5	139
	Sphorophila nigricollis	O	4					4
	Tiaris olivacea	O	179	29	37	23	5	273
	Volitinia jacarina	O	52	20	7	30	5	114
	Zonotrichia capensis	O	33	21	1	3		58
Falconidae	*Herpetotheres cachinnans*	F	2	1				3
	Micrastur ruficollis	B	1					1
	Milvago chimachima	O	4	3				7
Formicariidae	*Cercomacra tyrannina*	F	4					4
	Taraba major	O	1					1
	Thamnophilus bridgesi	F	1					1
Fringillidae	*Carduelis psaltria*	O	11		2	4		17
Furnariidae	*Automolus ochrolaemus*	F	1					1
	Synallaxis albescens	O	27	12	1	17	3	60
	Synallaxis brachyura	O	25	2	6	26	3	62
Icteridae	*Cacicus uropygialis*	F	1					1
	Icterus galbula	O	24	3	7	3	5	42
	Molothrus aeneus	O	1	1				2
	Psarocolius wagleri	F		1	6	2		9
	Quiscalus mexicanus	O	8	1				9
	Sturnella magna	O	1	2				3
Momotidae	*Momotus momota*	B	5	1	2	2	7	17
Parulidae	*Basileuterus rufifrons*	O	17		2	1	1	21
	Dendroica dominica	B		1				1
	Dendroica fusca	B	9	1	1			11
	Dendroica pensylvanica	B	96	14	21	9	5	145

APPENDIX (continued)

Family	Species	Habitat affiliation*	Edge	Plot type: Active pasture	Coffee	Fallow fields	Other†	Total individuals
	Dendroica petechia	O	24	3	16		1	44
	Dendroica virens	F		1				1
	Geothlypis aequinoctialis	O	3	4				7
	Geothlypis trichas	O	1					1
	Mniotilta varia	B	18	1	1	2	4	26
	Myioborus miniatus	B	1					1
	Oporornis formosus	F	1					1
	Oporornis philadephia	O	12		5	3		20
	Phaeothlypis fulvicauda	B	4					4
	Setophaga ruticilla	F	1		2			3
	Vermivora chrysoptera	F	1	1	1		1	4
	Vermivora peregrina	O	84	9	23	3	3	122
	Wilsonia pusilla	F	33	2	10	5	1	51
Picidae	*Dryocopus lineatus*	B	8	1	2	4		15
	Melanerpes rubricapillus	B	42	9	17	3	1	72
	Piculus rubiginosus	F		2				2
	Picumnus olivaceus	B	1			1		2
Pipridae	*Corapipo leucorrhoa*	F	1					1
	Manacus aurantiacus	F	6					6
Psittacidae	*Amazona autumnalis*	B	1					1
	Aratinga finschi	B	27	35	21	7		90
	Brotogeris jugularis	B	32	2	1			35
	Pionus menstruus	B	1					1
	Pionus senilis	B	99	1		3		103
Rallidae	*Aramides cajanea*	B	2		1			3
Ramphastidae	*Aulacorhynchus prasinus*	B	3			1		4
	Pteroglossus frantzii	F	53	7	4	1		65
Sylviidae	*Polioptila plumbea*	B	14		22	2		38
Thraupidae	*Chlorophanes spiza*	B	15		1			16
	Chlorospingus ophthalmicus	B	12		3	1		16
	Cyanerpes cyaneus	B	6	2	1			9
	Dacnis venusta	B	32	6	11	4		53
	Euphonia elegantissima	B	13					13
	Euphonia laniirostris	B	2	3	1			6
	Euphonia luteicapilla	B	4		4			8
	Piranga flava	F			1			1
	Piranga rubra	B	5				2	7
	Ramphocelus costaricensis	O	221	14	45	40	5	325
	Tachyphonus rufus	B	14	1	7	7		29
	Tangara guttata	F	4		2			6
	Tangara gyrola	F	13	1				14
	Tangara icterocephala	B	46	3	17	3	2	71
	Tangara larvata	B	138	15	45	15		213
	Thraupis episcopus	O	243	33	68	40	10	394
	Thraupis palmarum	O	24	1	3	1	1	30
Tityridae	*Pachyramphus aglaiae*	F	1	1				2
	Tityra semifasciata	B	21	4	8	1		34
Trochilidae	*Amazilia edward*	O	1					1
	Amazilia tzacatl	B	70	5	14	3	6	98
	Campylopterus hemileucurus	F	1		1			2
	Chlorostilbon canivetii	B	6		2			8

APPENDIX (continued)

Family	Species	Habitat affiliation*	Edge	Plot type: Active pasture	Coffee	Fallow fields	Other†	Total individuals
	Florisuga mellivora	B	2		2			4
	Heliomaster longirostris	O	4	1				5
	Phaethornis guy	F	2		1			3
	Phaethornis longuemareus	F	1		1			2
Troglodytidae	*Thryothorus modestus*	O	44	3	10	12	2	71
	Thryothorus rufalbus	F	1					1
	Thryothorus rutilus	B	14	1	2	1		18
	Troglodytes aedon	O	111	12	13	12	6	154
Trogonidae	*Trogon bairdii*	F	1					1
Turdidae	*Catharus aurantiirostris*	B	12		2		1	15
	Turdus assimilis	B	11		2	2		15
	Turdus grayi	B	145	13	42	17	6	223
Tyrannidae	*Camptostoma obsoletum*	B	1					1
	Capsiempis flaveola	O	5		4	2		11
	Contopus sordidulus	B	1					1
	Contopus virens	B	4	2				6
	Elaenia chiriquensis	O	27	1	13	9	1	51
	Elaenia flavogaster	O	55	5	5	9	2	76
	Elaenia frantzii	O	6	3		1		10
	Elaenia sp.	–	3					3
	Empidonax sp.	–	6	3	2	1		12
	Legatus leucophaius	O	3		1			4
	Megarhynchus pitangua	B	20	4	4	1	1	30
	Myiarchus crinitus	F	1					1
	Myiarchus tuberculifer	F	1					1
	Myiodynastes luteiventris	B	2		3			5
	Myiodynastes maculatus	B	3		2	1		6
	Myiopagis virdicata	B	4					4
	Myiophobus fasciatus	O	5	1	2	6		14
	Myiozetetes granadensis	O	21			4	4	29
	Myiozetetes similis	O	118	10	15	14	13	170
	Pitangus sulphuratus	O	8		1	1		10
	Todirostrum cinereum	O	39	1	5	5	1	51
	Todirostrum sylvia	B	2		1		1	4
	Tolmomyias sulphurescens	F	1					1
	Tyrannus melancholicus	O	81	18	7	8	29	143
	Zimmerius vilissimus	B	37	3	4	3		47
Vireonidae	*Hylophilus decurtatus*	F	1					1
	Vireo flavifrons	F	22	2		1	1	26
	Vireo philadelphicus	B	1				1	2
	Vireolanius pulchellus	F			1	1		2
Total			3214	419	712	494	167	5006

*Habitat affiliation assessed from Gretchen Daily, Salley Bailey and James Zook (unpublished data), Stiles & Skutch (1989), and personal observations: F = restricted to forested habitats (including edges of small fragments); O = restricted to open habitats; B = occurs in both forested and open habitats of the countryside.

†Includes individuals observed in minor plot types and those heard but not seen.