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SPECIES RICHNESS OF UNDERSTORY BIRDS IN DIFFERENT HABITATS OF THE CERRADO REGION OF SOUTHEASTERN BRAZIL

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Abstract. The cerrado region of South America is a savanna-like biome encompassing more than 1.8 million km^2 of a complex mosaic of xeric and mesic habitats. Here we test the hypothesis that the mesic habitats of the cerrado play a major role in the maintenance of species diversity in the entire biome. Richness patterns of small birds for both habitats in three different areas of the cerrado are shown. Bird censuses were conducted by relying on the use of standard mist-nets for captures. A first-order jackknife estimator of species richness showed that xeric habitats do support a higher number of species than mesic ones. The present data show xeric habitats to be as important as mesic ones for the maintenance of diversity in the cerrado. This is because (1) xeric habitats receive a higher number of migratory birds during the wet season, and (2) birds that depend on forests also seem to be dependent on xeric habitats. The present findings also support a previous untested prediction that drier habitats play an important role in sites located in the peripheral areas of the cerrado region. A possible explanation is the higher habitat heterogeneity in those areas. *Accepted 21 August 2007*.

Key words: *cerrado*, *diversity*, *gallery forest*, *habitat heterogeneity*, *savanna*.

INTRODUCTION

The cerrado region of South America encompasses more than 1.8 million km^2 (Ab'Sáber 1977) and is nowadays regarded as the most threatened biome in South America (Myers *et al*. 2000). The region includes most areas of Central Brazil, northeastern Paraguay, and eastern Bolivia. Most of the region is covered by savanna-like vegetation known as "cerrado" (see Eiten 1972 for a detailed description of the area) and holds an extremely rich diversity of organisms (Mittermeier *et al*. 1999). However, such high diversity is not uniformly distributed across the region as this biome comprises a complex mosaic of xeric (dry open grasslands, open and dense scrublands, referred to as "campo cerrado", "cerrado *sensu stricto*" and "cerradão" respectively) and mesic (tall evergreen forests along watercourses referred to as gallery forests, as well as semi-deciduous and deciduous dry forest patches growing in rich-soil areas) habitats (Eiten 1972, Ribeiro & Walter 1998). Such a diversity of environmental conditions may cause different patterns of species diversity across this landscape.

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It has been suggested that gallery forests play a major role in the maintenance of species diversity in the entire cerrado region (Redford & Fonseca 1986). These authors argue that gallery forests have been present in the cerrado for a long time and have served as mesic enclaves, making xeric adaptations on the part of mammalian species unnecessary. Alho (1982) and Mares & Ernest (1995) have also shown that the tropical gallery forests of central Brazil support a small-mammal fauna that is at least as rich and complex as that of any other tropical site previously examined, and may support higher densities than those reported for other studied sites.

Despite a relative consensus on the importance of mesic habitats to the maintenance of diversity in the cerrado, the hypothesis has been largely untested for taxa other than non-volant mammals. Silva (1995a) has undertaken the most extensive review of the cerrado birds, and found that approximately half of the species are forest dependent, i.e. mesic dependent, as a low percentage of endemic ones (3.8%). Also, the author argues (citing his own unpublished data) that gallery forests play an important role in sites located on the plateaus of the cerrado region, where

such forests are sometimes the only forested habitat available. However, dry forests, and not gallery forests, play a major role in sites located in the peripheral depressions of the cerrado region (Silva 1995a), leading to the suggestion that the view advanced by mammalogists, whereby gallery forests would play a major role in maintaining species richness in the cerrado, could possibly be biased.

This study aims at describing patterns of species richness of small understory birds in xeric and mesic habitats in three different areas in the peripheral depressions of the cerrado biome in southeastern Brazil. Understory birds represent a significant portion of the bird community (Karr 1976).

If mesic habitats are of major importance for the maintenance of diversity in the cerrado then, (1) species richness (SR) in those habitats should be higher when compared with that of xeric environments' and (2) the distribution of forest-dependent species should be biased towards mesic habitats.

METHODS

We follow the "morphoclimatic domain of the cerrados" delimited by Ab'Sáber (1977) as a synonym for the cerrado region, as accepted by several authors (Redford & Fonseca 1986, Mares & Ernest 1995, Silva & Bates 2002).

The climate in the cerrado can be described as tropical and highly seasonal, with a dry period ranging from May to October, and annual rainfall varying from 1200 to 2000 mm depending on locality (Nimer 1979). The region lies on a vast plateau separated by a network of peripheral depressions (Silva 1997). On this plateau, humid forests are restricted to narrow fringes along rivers and streams, forming a dense network within a large matrix of open grassland fields known as "campo cerrado" (Silva 1997, Ribeiro & Walter 1998). The peripheral depression harbors a vegetation mosaic ranging from open grassland fields, open and dense scrubland, deciduous (dry) and semi-deciduous forests, and large gallery forests (Silva 1997).

Fieldwork was carried out in three private areas holding natural patches of scrubland, dry forest, and gallery forest within the peripheral depressions of the cerrado region in Minas Gerais state, southeast Brazil, from July 2001 to October 2003 (Figure 1). The climate for the three areas is somewhat similar, being highly seasonal with a dry period from April to September and a rainy period from October to March. The vegetation types were classified according to Ribeiro & Walter (1998). We sampled one plot at a "cerrado *senso stricto*" site (a xeric site referred to here as "scrubland sample") and another plot at a forest site (a mesic site referred to here as "forest sample") in each one of the three areas: Fazenda Corredor, Fazenda Brejão, and Fazenda Santa Cruz.

Fazenda Corredor. This is a 12556-ha area in the municipality of Bocaiúva (17°06'S, 43°48'W). Total annual precipitation is around 1048 mm. It is a eucalyptus farm that holds 2199 ha of natural patches, which are 35.7 % cerradão, 25.5 % cerrado sensu stricto, and the remaining areas with deciduous and gallery forests. The Fazenda Corredor is located in the upper Rio Jequitinhonha basin, and is affected by the influence of "caatinga", a semi-arid biome typical of inland northeastern Brazil characterized by very low rainfall (Ab'Sáber 1977, Sampaio 1995). Three bird species typical of caatinga (according to Sick 1993 and 1997) occur in the area: *Sakesphorus cristatus* (Silvery-cheeked Antshrike), *Myrmorchilus strigilatus* (Striped-backed Antbird), and *Aratinga cactorum* (Cactus Parakeet). The scrubland sample (CCR) (17°23'33"S, 43°54'26"W – altitude: 922 m) was taken in an area of dense scrubland, with a canopy cover of about 50 to 70 %, and tree mean height between 5 and 8 m. The forest sample (MCR) (17°23'22"S, 43°53'46"W – altitude: 871 m) was taken in a dry forest holding a small watercourse, present only in the wet season. The forest is characterized as semi-deciduous due to the mean height of the trees falling between 15 and 25 m, tree trunks predominantly straight, and 50 % of canopy cover in the dry season.

Fazenda Brejão. This is a 36000-ha area in the municipality of Brasilândia de Minas (17°00'S, 46°00'W). Total annual precipitation is around 1192 mm. Fazenda Brejão holds 23383 ha of undisturbed cerrado, and is considered a priority area for the conservation of this biome (Costa *et al.* 1998). It is characterized mainly by cerradão, cerrado sensu stricto, palm tree groves (*Mauritia flexuosa*) and gallery forests along the Rio Paracatu (a major tributary of middle the Rio São Francisco basin). The scrubland sample (CBJ) (17° 01'45"S, 45°54'06"W – altitude: 556 m) was taken in a plot of cerradão as described before. The 'forest sample' (MBJ) (17°04'28"S, 45°54'14"W – altitude: 554 m) was taken in a patch of gallery forest along the Rio Paracatu. The plot is characterized by a tall

evergreen forest canopy 20 to 25 m high and a partially open understory.

Fazenda Santa Cruz. This is a 2977-ha area in the municipality of Felixlândia (18°45'S, 44°53'W). Total annual precipitation is around 1189 mm. Fazenda Santa Cruz is located on the edge of Três Marias reservoir and holds 916 ha of natural patches of cerrado sensu stricto, cerradão, campo cerrado and semi-deciduous, and deciduous forests. The scrubland sample (CSC) (18°43'22"S, 45°03'11"W – altitude: 723 m) was taken in a plot of cerradão with short trees of 3 to 7 m high, dense undergrowth of small shrubs, and herbaceous vegetation. The forest sample (MSC) (18°44'36"S, 45°02'29"W – altitude: 666 m) was taken in a plot of semi-deciduous forest, harboring a dense understory with a high number of lianas and a canopy reaching 10 to 12 m. A small watercourse is also present in this sample area during the wet season.

Birds were censused using mist-nets that were 12 m long, 2.5 m high, and had a 36-mm-square mesh. This method is biased towards small birds weighing from 2.5 g (hummingbirds) to 300 g (small raptors) that live and/or forage mainly at low height (Ralph *et al*. 1996, Rodrigues *et al*. 2000). "Understory birds" account for a large and representative portion of the bird community (Karr 1976, 1981). The method is aimed at enabling the comparison of areas since it assumes that all species have the same probability of being captured. Moreover, and most importantly, it is the only bird census method that yields data that are less dependent on the observer (Bibby *et al*. 1993).

We used 12 standard mist-nets, from 06:00 h to 13:00 h for two consecutive days in the interior of each plot. Each plot was sampled six times throughout the year, covering the four seasons. The captured birds were identified to species level using recognized field guides (Schauensee 1970, Grantsau 1988, Ridgely & Tudor 1989, and 1994, Sick 1997, Souza 2002). Each bird was banded with a metal ring marked with a unique number and was subsequently released nearby, allowing individual identification when recaptured.

We regarded each net as an independent sample unit, so we could estimate species richness through extrapolation using a first-order jackknife estimator (Colwell & Coddington 1994, Gotelli & Colwell 2001). Although capture rates can vary between nets, this estimator was observed to be more precise and less biased than others due to its rarefaction properties, and therefore can be used for comparing species richness between different areas (Palmer 1990). The use of such a method yields estimated species richness values within 95% confidence intervals, thereby allowing a direct statistical comparison between species richness in the different areas. Species richness values were extracted using 'EstimateS' (Colwell 1997).

Chi-square statistics were used to test the degree of habitat dependence of the bird species. The forest dependence classification for each species was assigned according to Silva (1995a) as: "independent" for those species occurring in open vegetation; "semi-dependent" for those occurring in both open and forested vegetation, and "dependent" for those species found mainly in forest habitats.

RESULTS

We recorded 107 bird species from a total of 1389 individuals after 9716 net-hours. Of these, 725 birds belonging to 85 species came from xeric habitats, whereas mesic habitats yielded 664 birds belonging to 85 species (Table 1 and Appendix).

The sample-effort curves, produced by jackknife estimation, showed a tendency for stabilization and a higher value of richness for xeric habitats (Figure 1).

TABLE 1. Total number of species and individuals captured in xeric and mesic habitats in three areas (Fazenda Corredor, F. Brejão and F. Santa Cruz) of the cerrado region of southeastern Brazil from September 2001 to October 2002.

	Corredor			Brejão			Santa Cruz			Total	
	Total	Mesic	Xeric	Total	Mesic	Xeric	Total	Mesic	Xeric	Mesic	Xeric
Number of species	76	57	66	60	44	36	59	37	44	85	85
Number of individuals	646	341	305	400	189	211	343	134	209	664	725

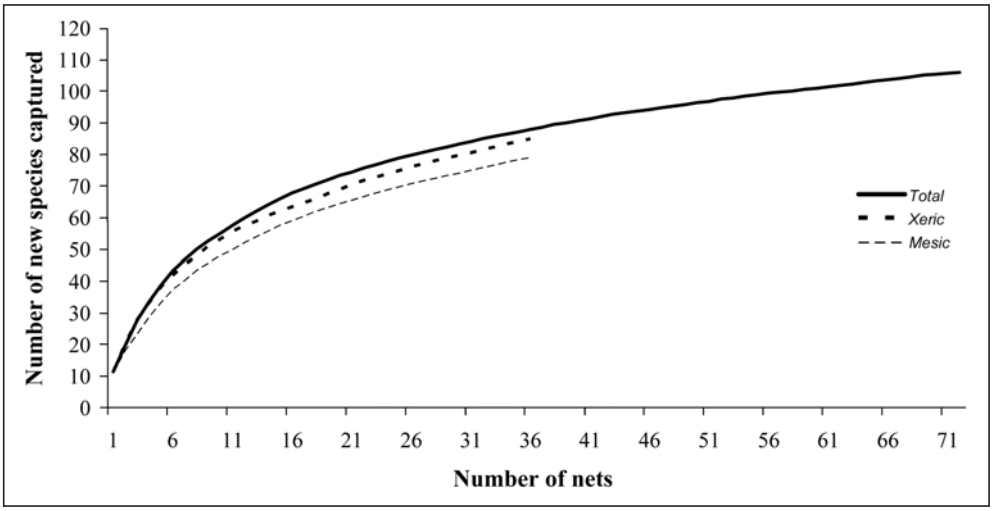

FIG. 1. Estimated species accumulation curve plotted against the sample effort (number of nets) for xeric and mesic habitats sampled in three areas of the cerrado region of southeastern Brazil from September 2001 to October 2003.

The estimated species richness shows that xeric habitats support a higher number of species than mesic ones (Figure 2).

The proportion of migratory species was also found to be higher in xeric than in mesic habitats (Table 2), and there is no difference among the habitat types, xeric and mesic, in relation to the proportion of habitat-dependent species (Table 3).

DISCUSSION

Our data show that xeric habitats can be as rich as mesic ones in the cerrado biome, contradicting the

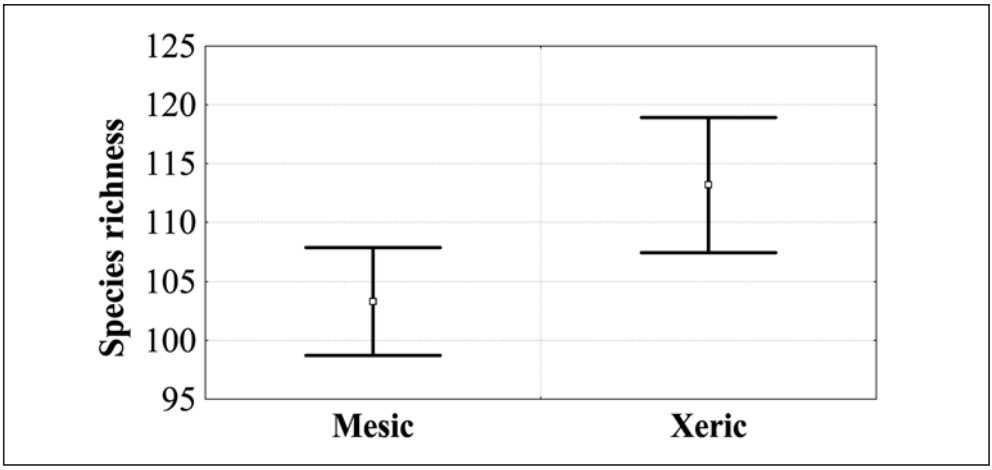

FIG. 2. Species richness estimation (± SD) for each study plot of xeric (CCR, CBJ, CSC) and mesic (MCR, MBJ, MSC) habitats sampled in three areas of the cerrado region of southeastern Brazil from September 2001 to October 2003.

TABLE 2. Number of migratory species and individuals captured in xeric and mesic habitats in three areas of the cerrado region of southeastern Brazil from September 2001 to October 2002.

Total number	Xeric	Mesic	total
Individuals	64 (9%)	20 (3%)	84
Migratory species	7 (8%)	4 (5%)	8

evidence shown for small mammals (Alho 1982, Redford & Fonseca 1986, Mares & Ernest 1995). The present results support a previous prediction that drier habitats, and not gallery forests, play an important role in sites located at the peripheral depressions of the cerrado region (Silva 1995a). However, the original prediction made by Silva regarded dry forests as more important than scrubland habitats. Here we show the importance of scrublands for the maintenance of species richness of small understory birds. This is because estimated species richness is higher in xeric than mesic habitats. Also, we found no relationship between both habitats in the degree of habitat specialization of their corresponding bird species. Mesic habitats did not appear to hold higher numbers of forest-dependent species than expected by chance, at least for small understory birds. Certainly, forest canopy birds, which undoubtedly constitute a high proportion of the bird community of the mesic areas, were not sampled. However, the aim of this work was to focus on understory birds. It is known that tropical birds are also strata-dependent (Stotz *et al.* 1996, Terborgh *et al.* 1990) and therefore those that live in the canopy of mesic sites do not use lower strata in xeric ones.

Our findings are also in agreement with a recent study that focused on the entire bird community in an area within the plateau of the cerrado region, where it was found that cerrado *sensu strictu* holds a high diversity of birds (Tubelis *et al.* 2004).

Why communities of small birds are richer in xeric than in mesic habitats deserves an explanation.

(1) As shown above, xeric habitats received a higher number of migratory birds during the wet season, which highlights the importance of xeric habitats for the maintenance of migratory communities of small birds. It has been argued that the seasonal abundance of insects contributes significantly to the variation in richness and abundance of birds throughout the year (Macedo 2002). Most of these small migrants reaching the southeast Brazil during the austral summer come from the Amazon basin looking for the insect boom that occurs at the cerrado during the rainy season (Negret & Negret 1981, Sick 1993). Migratory behavior is more widespread in forest-independent species than in forest-dependent ones (see accounts in Stotz *et al.* 1996 and Sick 1993). At the study site we found eight migratory species, and most of them were forest-independent.

(2) Birds that depend on forests habitats also seem to be dependent on xeric habitats, a suggestion also made by Tubelis *et al.* (2004). These authors showed that the home ranges of forest birds include large patches of the dry scrubland surrounding the gallery forests. It has been suggested that in fact forest birds depend upon these xeric habitats more than was previously assumed. If so, the classification of these forest-dependent birds, as presented by Silva (1995a), should be revised.

Silva (1995a) has argued that dry forests, and not gallery forests, play a major role in sites located in the peripheral depressions of the cerrado region. This is because the habitat is much more heterogeneous in that area, and in fact, its borders are still disputed as being part of the cerrado. For instance, the gallery forests of the middle São Francisco river support a very distinct endemic avifauna (Silva & Straube 1996, Raposo 1997, De Lima 1999, Kirwan *et al.* 2001). The same is valid for the highlands of Espinhaço Range, a distinct region within the cerrado (Vasconcelos *et al.* 2003). In fact, most of the area covered by cerrado has not been adequately surveyed (Silva 1995b). As the number of professional ornithologists grows in Brazil, new localities for endemic species, and even new taxa, are being discovered (e.g. D'Angelo-Neto 2000, Vasconcelos *et al.* 2002, 2003, Rodrigues & Gomes 2004). For instance, between 1983 and 1998, 17 new bird species were described for Brazil. Of those, 14 species were found in localities close to

TABLE 3. Relationship of habitat dependence of small bird species occurring at xeric and mesic habitats in three areas of the cerrado region of southeastern Brazil from September 2001 to October 2002.

	Habitats		Chi^2	P
	Xeric	Mesic	(df = 1)	
Independent	14	15	0,88	0,35
Semi-dependent	34	27	0,35	0,56
Dependent	33	40	0,44	0,51

densely populated parts of southeastern Brazil (Vasconcelos *et al*. 2002). We still need to assess the impact of these findings on our diversity pattern analysis.

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APPENDIX. Relative abundance of captured birds at six areas of the cerrado region of Minas Gerais, southeastern Brazil from July 2001 to October 2003. Taxonomic order and names follows Sick (1993). Habitat dependence according to Silva (1995a): 1 – Independent; 2 – Semi-dependent; 3 – Dependent (see Methods for details); (*) – Migratory species.

Families and Species	English name	Number of individuals captured	Habitat dependence
TINAMIDAE			
Crypturellus parvirostris	Small-billed Tinamou	1	1
ACCIPITRIDAE			
Accipiter striatus	Sharp-shinned Hawk	1	2
COLUMBIDAE			
Columba picazuro	Picazuro Pigeon	1	2
Columbina talpacoti	Ruddy-ground Dove	3	1
Claravis pretiosa *	Blue-ground Dove	5	2
Scardafella squammata	Scaled Dove	8	1
Leptotila verreauxi	White-tipped Dove	13	2
STRIGIDAE			
Otus choliba	Tropical Screech Owl	1	2
CAPRIMULGIDAE			
Hydropsalis brasiliana	Scissor-tailed Nightjar	4	1

Appendix continued

Families and Species	English name	Number of individuals captured	Habitat dependence
TROCHILIDAE			
Phaethornis pretrei	Planalto Hermit	5	2
Campylopterus largipennis	Gray-breasted Sabrewing	1	3
Eupetomena macroura	Swallow-tailed Hummingbird	12	1
Anthracothorax nigricollis *	Black-throated Mango	1	2
Chlorostilbon aureoventris	Glittering-bellied Emerald	14	2
Thalurania furcata	Fork-tailed Woodnymph	27	2
Amazilia fimbriata	Glittering-throated Emerald	44	2
GALBULIDAE			
Galbula ruficauda	Rufous-tailed Jacamar	2	2
BUCCONIDAE			
Nystalus maculatus	Spot-backed Puffbird	7	2
Nonnula rubecula	Rusty-breasted Nunlet	11	3
PICIDAE			
Picumnus cirratus	White-barred Piculet	1	2
Picumnus albosquamatus	White-wedged Piculet	5	2
Piculus chrysochloros	Golden-green Woodpecker	5	3
Veniliornis passerinus	Little Woodpecker	7	2
Campephilus melanoleucos	Crimson-crested Woodpecker	1	3
FORMICARIIDAE			
Taraba major	Great Antshrike	3	2
Sakesphorus cristatus	Silvery-cheeked Antshrike	23	3
Thamnophilus punctatus	Eastern Slaty Antshrike	57	3
Thamnophilus caerulescens	Variable Antshrike	1	3
Myrmorchilus strigilatus	Striped-backed Antbird	10	2
Herpsilochmus atricapillus	Black-capped Antwren	4	3
Formicivora melanogaster	Black-bellied Antwren	9	2
Pyriglena leucoptera	White-shouldered Fire-eye	8	3
CONOPOPHAGIDAE			
Conopophaga lineata	Rufous Gnateater	8	3
FURNARIIDAE			
Synallaxis frontalis	Sooty-fronted Spinetail	22	3
Poecilurus scutatus	Ochre-cheeked Spinetail	23	3
Hylocryptus rectirostris	Henna-capped Foliage-gleaner	3	3
Xenops rutilans	Streaked Xenops	2	3
DENDROCOLAPTIDAE			
Sittasomus griseicapillus	Olivaceous Woodcreeper	36	3
Xiphocolaptes albicollis	White-throated Woodcreeper	1	3
Dendrocolaptes platyrostris	Planalto Woodcreeper	15	3
Lepidocolaptes angustirostris	Narrow-bellied Woodcreeper	16	1
Lepidocolaptes squamatus	Scaled Woodcreeper	19	3

Appendix continued

Families and Species	English name	Number of individuals captured	Habitat dependence
TYRANNIDAE			
Camptostoma obsoletum	Southern Beardless-Tyrannulet	10	1
Phaeomyias murina	Mouse-colored Tyrannulet	43	1
Myiopagis viridicata	Greenish Elaenia	30	3
Elaenia flavogaster	Yellow-bellied Elaenia	1	2
Elaenia parvirostris *	Small-bellied Elaenia	1	1
Elaenia cristata	Plain-crested Elaenia	14	1
Elaenia obscura	Highland Elaenia	1	3
Elaenia chiriquensis	Lesser Elaenia	18	1
Leptopogon amaurocephalus	Sépia-capped Flycatcher	20	3
Hemitriccus margaritaceiventer	Pearly-vented Tody-Tyrant	40	2
Todirostrum latirostre	Rusty-fronted Tody-Flycatcher	1	3
Tolmomyias sulphurescens	Yellow-olive Flycatcher	12	3
Tolmomyias flaviventris	Yellow-breasted Flycatcher	15	3
Myiobius barbatus	Sulphur-rumped Flycatcher	4	3
Contopus cinereus	Tropical Pewee	2	3
Lathrotriccus euleri	Euler's Flycatcher	20	3
Cnemotriccus fuscatus	Fuscous Flycatcher	23	3
Knipolegus franciscanus	Caatinga Black-Tyrant	4	3
Casiornis rufa	Rufous Casiornis	27	3
Myiarchus ferox	Short-crested Flycatcher	23	2
Myiarchus tyrannulus	Brown-crested Flycatcher	34	2
Myiarchus swainsoni *	Swainson's Flycatcher	7	1
Pitangus sulphuratus	Great Kiskadee	1	1
Megarhynchus pitangua	Boat-billed Flycatcher	3	2
Myiozetetes similis	Social Flycatcher	1	2
Myiodynastes maculatus *	Streaked Flycatcher	26	3
Empidonomus varius *	Variegated Flycatcher	2	2
Tyrannus melancholicus *	Tropical Kingbird	3	1
Pachyramphus viridis	Green-backed Becard	1	2
Pachyramphus polychopterus	White-winged Becard	9	2
Tityra cayana	Black-tailed Tityra	1	3
PIPRIDAE			
Antilophia galeata	Helmet Manakin	3	3
Neopelma pallescens	Pale-bellied Tyrant-Manakin	13	3
CORVIDAE			
Cyanocorax chrysops	Plush-crested Jay	1	2
TROGLODYTIDAE			
Thryothorus leucotis	Buff-breasted Wren	3	3
Troglodytes aedon	House Wren	1	1

Appendix continued

Families and Species	English name	Number of individuals captured	Habitat dependence
MUSCICAPIDAE			
Polioptila plumbea	Tropical Gnatcatcher	2	3
Turdus rufiventris	Rufous-bellied Thrush	1	1
Turdus leucomelas	Pale-breasted Thrush	38	2
Turdus amaurochalinus *	Creamy-bellied Thrush	36	2
Turdus albicollis	White-necked Thrush	32	3
VIREONIDAE			
Cyclarhis gujanensis	Rufous-browed Peppershrike	25	2
Vireo chivi	Chivi Vireo	2	3
Hylophilus poicilotis	Rufous-crowned Greenlet	8	3
EMBERIZIDAE			
Basileuterus flaveolus	Flavescent Warbler	141	3
Basileuterus culicivorus	Golden-crowned Warbler	20	3
Basileuterus hypoleucus	White-bellied Warbler	18	3
Coereba flaveola	Bananaquit	2	2
Hemithraupis guira	Guira Tanager	5	3
Hemithraupis ruficapilla	Rufous-headed Tanager	1	3
Nemosia pileata	Hooded Tanager	1	3
Eucometis penicillata	Gray-headed Tanager	4	3
Tachyphonus rufus	White-lined Tanager	2	3
Thraupis sayaca	Sayaca Tanager	15	2
Thraupis palmarum	Palm Tanager	1	2
Euphonia chlorotica	Purple-throated Euphonia	12	2
Tangara cayana	Burnished-buff Tanager	33	1
Dacnis cayana	Blue Dacnis	2	2
Conirostrum speciosum	Chestnut-vented Conebill	3	3
Zonotrichia capensis	Rufous-collared Sparrow	8	1
Volatinia jacarina	Blue-black Grassquit	7	1
Arremon flavirostris	Saffron-billed Sparrow	3	3
Coryphospingus pileatus	Grey-pileated Finch	60	2
Saltator similis	Green-winged Saltator	43	2
Passerina brissonii	Ultramarine Grossbeak	6	2