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HABITAT SPECIALIZATION AND FORAGING BEHAVIOR BY BIRDS OF AMAZONIAN RIVER ISLANDS IN NORTHEASTERN PERU[1]

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Abstract. Roughly 15% of the rich Amazonian avifauna has been shown to be dependent on riverine habitats, particularly islands that form in the channels of the Amazon River and its largest tributaries. In northeastern Peru and southeastern Colombia, over 230 species have occurred on river islands, about 19 of which appear to be restricted to habitats found almost exclusively on islands, such as *Tessaria*-scrub and large tracts of *Cecropia* forest. Habitat specialization and foraging behavior were studied quantitatively for 31 bird species that used only terrestrial habitats on two study islands on the Napo River in northeastern Peru. Density estimates for residents on a small, *Tessaria*-dominated island, exceeded 160 birds/ha, a figure an order of magnitude greater than bird densities previously reported for forest habitats in the Neotropics. Obligate river island species showed a higher degree of microhabitat specialization than did nonobligate island species. Several of the most specialized species were found mainly in the *Tessaria* scrub or the understory of the *Cecropia* forest. Most of the species were primarily insectivorous, but several also took advantage of the abundant *Cecropia* fruit and were at least partially frugivorous. Little difference in the degree of foraging specialization was found between obligate and nonobligate island species, however, both groups were specialized with respect to foraging technique and substrate use. Water fluctuation of up to 20 m between seasons, completely flooding the young islands and the understory of the older islands, creates the need for species to be good colonizers, as does the natural, rapid, succession of vegetation on the islands from *Tessaria,* to *Cecropia,* to an older, more complex vegetation. Conservation plans for the Amazon basin should take into account the high dependency of species on riverine habitats, particularly islands.

Key words: Amazonia; habitat specialization; river islands; Napo River; foraging behavior; Peru; Tessaria *scrub;* Cecropia *forest.*

INTRODUCTION

Among the many factors thought to contribute to the high bird species richness in the Neotropics is the high diversity of habitat and microhabitat types, some of which are unique to tropical regions (Orians 1969, Karr 1976, Terborgh 1980b). Even more important is the increased degree of specialization on specific microhabitats, such as bamboo (Parker and Parker 1982, Remsen 1985), and foraging substrates, such as suspended dead leaves (Remsen and Parker 1984). Although bird species richness reaches its peak in *terra firme* forest, it is the contribution by habitats other than primary forest that elevates the richness to such high levels in western Amazonia. For example, it has been shown that more than 14% of the nonaquatic avifauna of the Amazon basin occurs only in riverine habitats (Remsen and Parker 1983).

Islands that form in the Amazon River and its larger tributaries, which are covered by early successional vegetation, constitute a large proportion of the total riverine habitat in Amazonia. After formation, these islands travel downstream, in a sense, by constant erosion of the older, upstream portions, and the constant increase in size by the deposition of sand and silt on the downstream ends. This constant change creates an array of early successional habitats on the islands. The use of and specialization on such habitats by Amazonian birds has remained poorly known (see Remsen and Parker 1983, Hilty and Brown 1986).

Exploratory visits to islands in the Napo River in northeastern Peru in 1982 with the Louisiana State University Museum of Natural Science (LSUMNS) revealed that the assemblage of landbird species on these islands was almost completely different from that found in *terra firme* forest on the "mainland" only 1–2 km away.

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Some species encountered on the islands were river-edge and second-growth species that were common on the mainland, but several appeared unique to the islands. Since 1982, extensive surveys of river-island and mainland habitats in northeastern Peru by the LSUMNS and Philadelphia Academy of Sciences suggested that as many as 19 bird species may be restricted to islands in this region of Amazonia. These surveys have added significantly to the growing knowledge of the distribution and natural history of these apparent obligate island species, some of which were known from only a few museum specimens and occasional sightings.

I returned to the Napo River in 1983 to study the birds found on river islands, particularly those species apparently restricted to the islands. My primary goals in this study were to: (1) enumerate the bird species using islands in upper Amazonia; (2) describe for the first time the habitat use and foraging behavior of some river-island birds; (3) evaluate the degree of ecological specialization among river-island birds; and (4) discuss how this unique bird assemblage persists in such a dynamic, ephemeral environment.

STUDY AREAS AND METHODS

ISLAND FORMATION AND HABITATS

Amazonian river islands are part of a continuous chain of islands that extends from eastern Brazil up the Amazon River and most of its larger tributaries as far as Ecuador and Peru. The islands studied here are "sandbar islands" that form in the river, as opposed to "'oxbow islands" that form when the river channel changes its course and isolates a portion of mainland forest. These two island types differ in vegetation complexity, but a very old sandbar island will eventually visually resemble an oxbow island in terms of vegetation complexity.

Water levels on the Amazon and Napo rivers in northeastern Peru fluctuate as much as 20 m between seasons due to runoff from the Andes (Gentry and Lopez-Parodi 1980; Peter Jenson, pers. comm.), and as a result of the dynamic nature of this system, river islands vary substantially in age and size. Three age classes of islands may be recognized (young, middle-aged, and old; as described below). Some islands are even-aged throughout and easy to classify as one of the three types, whereas others vary considerably in age from one end to the other (the down-river end being younger) and potentially have vegetation characteristics of all three island types.

River islands are formed during the low-water season (June–October), when sandbars are exposed and enlarged by the deposition of silt. During low water, vegetation grows rapidly on the exposed sandbars. At first, grass (*Paspalum*) covers the ground; this is later replaced by the composite shrub *Tessaria integrifolia* and a willow *Salix humboltiana* (Remsen and Parker 1983). These young islands may be completely covered by water during portions of the high-water season (November–May). As an island grows in age and size, it becomes dominated by monotypic stands of *Cecropia* forest. Although *Cecropia* sp. is a common tree of disturbed area throughout the Neotropics, stands of such large size are not characteristic of disturbed areas on the mainland. During the high-water season, the entire understory of the forest on middle-aged and old islands may be under water. Old islands are characterized by larger size and vegetation that resembles in complexity the *varzea* forest (seasonally inundated forest and permanently swampy forest usually bordering rivers; as described in Parker and Parker 1982) of the mainland.

Preliminary observations indicated that most of the poorly known island species were found primarily in two major habitat types: *Cecropia* (river-edge) forest, and *Tessaria* sandbar scrub, as described by Remsen and Parker (1983). My study focused on one middle-aged and one young island in the Napo River that contained both habitat types. My primary study site, visited daily between 2 June and 31 July 1983, was Ronsoco Island, located opposite the small village of Libertad, approximately 1 km east of the village of Negro Urco, 80 km north of Iquitos. According to local residents, Ronsoco was about 16 years old. Approximately 1 km by 0.25 km in size, this island was about equidistant between the two banks of the Napo (which was about 1.5 km wide at that point). Monotypic stands of *Cecropia* ranging from 5 to 13 m tall were prevalent on the island, with an occasional emergent *Mimosa* sp. A distinct middle-story layer consisted of a "broad-leafed" tree (identification unknown) that ranged from 4 to 7 m in height. The understory was dominated by *Heliconia* sp. thickets and a vine (*Ipomea* sp.). Shorter *Cecropia* forest was also present on Ronsoco and was characterized

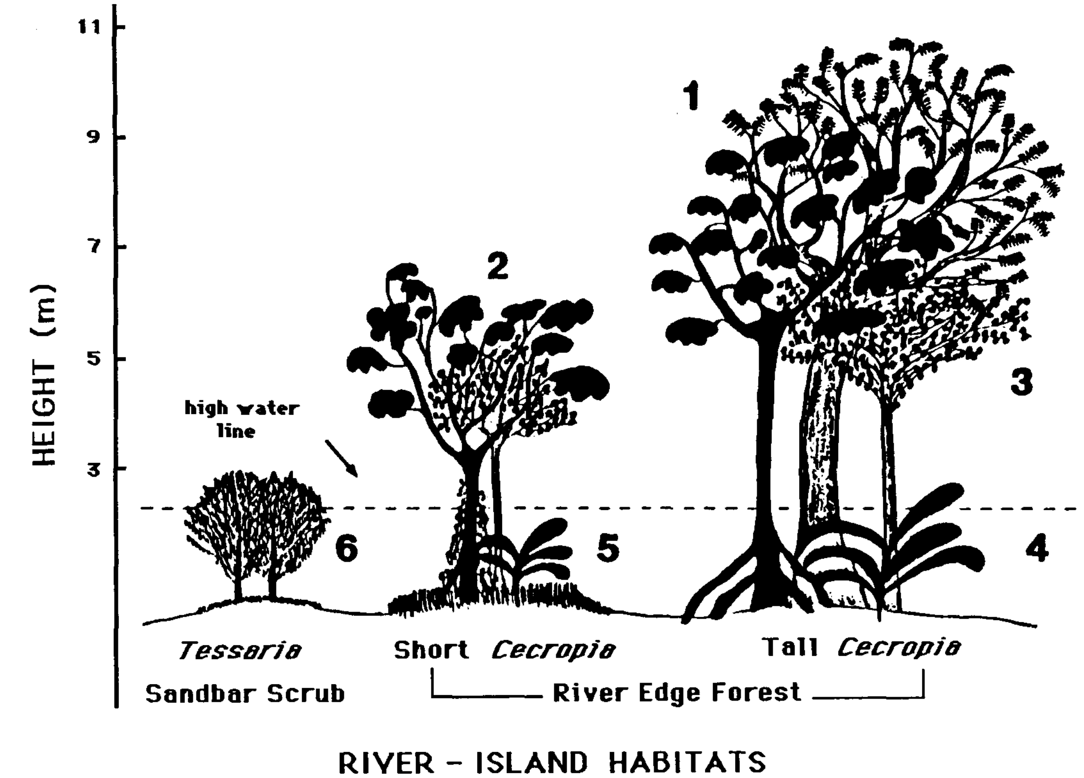

FIGURE 1. A diagrammatic sketch of river-island microhabitats: (1) canopy of tall *Cecropia* forest; (2) canopy of short *Cecropia* forest; (3) middle story of tall *Cecropia* forest; (4) understory of tall *Cecropia* forest; (5) understory of short *Cecropia* forest; (6) early successional *Tessaria* scrub. Note the high-water line that indicates which habitats are completely covered during high water.

by even-aged trees 5 to 7 m tall, the lack of a distinct middle-story, and an understory of vines and grass, with few *Heliconia.*

The second study site was Tuhuayo Island, only 130 m by 30 m, which was equidistant between Ronsoco Island and Negro Urco on the mainland. Tuhuayo, only 2 years old according to local residents (in 1982 it was a grass-covered sandbar), was typical of a young island in an early successional stage. Vegetation structure was simple on this island compared with that of older islands, with the dominant plant species *Tessaria integrifolia,* which attained a maximum height of 3 m. A lesser amount of *Salix humboltiana* was common along the edge of the riverbank, with some individuals reaching a height of 5 m. *Bacharis* sp. was also prevalent on the downstream end of the island, as were many sapling *Cecropia* scattered among the *Tessaria.* Tuhuayo was visited on 10 days, on five of which complete censuses of species and individuals were taken.

Based on the structure of the vegetation on the two islands, I divided the two macrohabitats (river-edge and sandbar scrub) into six microhabitats that might be recognized by birds (Fig. 1): (1) canopy of tall *Cecropia* forest; (2) canopy of short *Cecropia* forest; (3) middle-story of tall *Cecropia* forest; (4) understory of tall *Cecropia* forest; (5) understory of short *Cecropia* forest; and (6) *Tessaria* scrub. Ronsoco was a mosaic of tall and short *Cecropia* forest, as well as small patches of *Tessaria* scrub. Tuhuayo was covered entirely by *Tessaria* scrub.

AVIAN HABITAT USE AND FORAGING

To establish the status of river-island species in mainland habitats, and to determine which species were restricted to islands in this region

TABLE 1. List of obligate river-island species found in western Amazonia. Some of the species listed here were encountered too infrequently to be included in the quantitative portion of this paper.

Blue-rumped Parrotlet	*Forpus xanthopterygius*
Olive-spotted Hummingbird	*Leucippus chlorocercus*
Pale-billed Hornero	*Furnarius torridus*
Lesser Hornero	*F. minor*
White-bellied Spinetail	*Synallaxis propinqua*
Red-backed Spinetail	*Cranioleuca vulpina*
Red-and-white Spinetail	*Certhaixis mustelina*
Castlenau's Antshrike	*Thamnophilus cryptoleucus*
Leaden Antwren	*Myrmotherula assimilis*
Ash-breasted Antbird	*Myrmoborus lugubris*
Black-and-white Antbird	*Myrmochanes hemileucus*
Brown Elaenia	*Elaenia pelzelni*
River Tyrannulet	*Serpophaga hypoleuca*
Lesser Wagtail-Tyrant	*Stigmatura napensis*
Fuscous Flycatcher	*Cnemotriccus fuscatus*
Riverside Tyrant	*Knipolegus orenocensis*
Bicolored Conebill	*Conirostrum bicolor*
Pearly-breasted Conebill	*C. margaritae*

of Amazonia, I used data from three field expeditions to northeastern Peru by the LSUMNS, an unpublished species list for a tourist lodge on the Napo River (Explornapo Lodge) compiled by Theodore A. Parker, III, unpublished field notes of J. V. Remsen, Jr. from Monkey Island and adjacent *varzea* forest, near Leticia Colombia, from 1974–1975, and my own experience from fieldwork on the Napo and Amazon rivers spanning 4 years. This included visits to more than 10 islands representing all age classes. Any species recorded solely from river islands during these periods of observation is considered here to be an obligate island species.

During my own visits to the two main study islands, at the initial point of observation of each bird, I recorded the following: bird species; tree species; tree height; distance from ground; and distance from canopy. If an individual was seen foraging, I also recorded foraging technique (glean, sally, hover, lunge, hang, or hammer) and foraging substrate (leaf, bark, fruit, flower, grass, ground, or air). Data were not (knowingly) collected on the same individual during the same day. For each observation, I placed the individual into one of the six microhabitats base upon its location within the vegetation strata. Voucher specimens for all study species collected on my study sites and other river islands on the Amazon River were deposited at the LSUMNS.

To evaluate specialization by obligate and nonobligate island species with respect to habitat and foraging parameters, I first examined frequency distributions of observations for each variable. I then arbitrarily chose a value of 75% or greater use of an ecological category to represent "specialization" on that category. In addition, niche breadths were calculated using the formula $B = 1/[np_i^2]$ where p_i is the proportion in category i, and n is the total number of categories for the variable under consideration (Levins 1968), for each of the following variables: plant species; foraging height; foraging technique; and foraging substrate.

RESULTS

COMPOSITION OF RIVER-ISLAND AVIFAUNA

In this part of Amazonia, at least 18 species seemed to be restricted to river islands (hereafter obligate island species; see Table 1). Of these, 14 were included in the quantitative portion of my study. During more than 8 months of fieldwork along the Napo and Amazon rivers in northeastern Peru by the LSUMNS that included extensive collecting in all habitats, not one individual of any obligate island species was recorded off islands.

About 231 species have been recorded on river islands in northeastern Peru and southern Colombia (Appendix). Of these, only 3% have been recorded in *terra firme* forest on the mainland (Table 2). A far greater proportion of river-island species was found in other mainland habitats; 33% of the species also occurred in secondary woodland or second-growth, 25% occurred in *varzea* (seasonally flooded forest), 40% occurred in water-dependent (riverine) habitats that included river, lake, and stream margins, sandbars, and marsh; and at least 14% were seen as aerial transients, that included both foraging and nonforaging birds that flew over the islands. Virtually all of the species recorded on river islands between May and August were residents in this region of Amazonia, with the exception of the occurrence of several "austral" migrants (i.e., three species of *Elaenia*; see Appendix). Between August and April, several North American species may use river islands, particularly shorebirds that probably use the rivers as migratory pathways (Appendix).

TABLE 2. Bird species composition among three age classes of Amazonian river islands. Numbers represent the percentage of species found on a particular class of island (left hand column) and also found on the other two island classes (across the top). Note that some species are found on more than one age class of island.

		Island age		
Island age	No. species	Young	Middle-aged	Old
Young	62	–	83%	37%
Middle-aged	143	31%	–	63%
Old	166	13%	59%	–

Most of the obligate island species are representatives of genera typically found in open habitats. Those found in open shrubby habitats included: *Leucippus* (Trochillidae), *Furnarius* and *Certhiaxis* (Furnariidae), and *Elaenia, Stigmatura,* and *Serpophaga* (Tyrannidae), whereas, others that were found in a mixture of forest and open habitats included *Synallaxis* and *Cranioleuca* (Furnariidae), *Thamnophilus* (Formicariidae), *Cnemotriccus* (Tyrannidae), and *Conirostrum* (Coerebidae). Only *Myrmotherula* and *Myrmoborus* (both Formicariidae) can be considered mostly forest genera.

Several families or subfamilies of forest birds were absent or poorly represented on river islands including quail (Odontophorinae), trumpeters (Psophiidae), motmots (Momotidae), trogons (Trogonidae), tapaculos (Rhinocryptidae), and gnatcatchers (Polioptilinae). Equally striking is that only one of seven toucans (Ramphastidae), three of 16 woodcreepers (Dendrocolaptidae), seven of 56 antbirds (Formicariidae), one of 11 manakins (Pipridae), and nine of 27 tanagers (Thraupidae), found in this region of Amazonia were found on islands. Among the better-represented taxa were flycatchers (Tyrannidae; 38 of 72 species) and icterids (Icterinae; 11 of 15 species).

Bird species composition on young islands was more similar to middle-aged islands than to old islands (Table 2). A higher percentage of species found on middle-aged islands were also found on old islands, as opposed to young islands. A similarly high percentage of species found on old islands were also found on middle-aged islands, with very few having been recorded on young islands (Table 2).

More striking is the comparison between the number of bird species found on the three age classes of islands and the various mainland habitats (Table 3). Of the 62 species recorded from young islands, most were found either in secondary habitats or riverine habitats on the mainland, whereas none was found in *terra firme* forest, and only one was found in *varzea.* As on young islands, a high percentage of species that occurred on middle-aged islands were also found in secondary habitats on the mainland, but more species were also found in *varzea.* The forest on old islands visually resembled mainland *varzea* forest, and a much higher percentage of the old island species also occurred in *varzea.* In general, the bird-species composition on islands resembled the composition in the riverine habitats (river, lake, and stream margins, sandbars, etc.) on the mainland with at least 40% of the island species occurring there.

During June and July 1983, I found 110 species on the two study islands. Of these, sufficient sample sizes of observations of 31 species were obtained for quantitative analysis (Table 4). Many additional nonpasserines that visited the islands were eliminated from the study because they infrequently used the terrestrial habitats, or were

TABLE 3. Number of bird species found on three age classes of river islands and also found in various mainland habitats. *Terra firme* refers to upland forest that is never flooded. *Varzea* refers to seasonally flooded forest. Secondary habitats are influenced by man, such as second-growth and older secondary woodland. Riverine habitats include river, lake, and stream margins, open river, sandbars, and marsh. Aerial refers to species that were seen flying over islands (foraging and nonforaging). Numbers in parentheses are percentages of species on that particular age class of island. Rows add up to greater than 100% because some species occupy more than one habitat.

		Mainland habitats				
Island age	No. species	*Terra firme*	*Varzea*	Secondary habitats	Riverine habitats	Aerial
Young	62	0 (0%)	1 (1%)	23 (29%)	48 (60%)	10 (12%)
Middle-aged	143	4 (3%)	25 (17%)	63 (44%)	47 (33%)	11 (8%)
Old	166	7 (4%)	51 (31%)	53 (32%)	77 (46%)	17 (10%)
Total	231	8 (3%)	58 (25%)	76 (33%)	92 (40%)	33 (14%)

TABLE 4. Frequency of observations within microhabitats: (1) canopy of tall *Cecropia* forest; (2) canopy of short *Cecropia* forest; (3) middle story of tall *Cecropia* forest; (4) understory of tall *Cecropia* forest; (5) understory of short *Cecropia* forest; and (6) *Tessaria* scrub. Also, frequency of observations in various plant species: CP = *Cecropia*; M = *Mimosa*; BL = broad-leafed; T = *Tessaria*; S = *Salix*; P = *Paspalum*; V = vines (*Ippomoea*); O = other. *n* = sample size.

		Microhabitat						Plant species							
Bird species	*n*	1	2	3	4	5	6	CP	M	BL	T	S	P	V	O
Obligate island species															
Leucippus chlorocercus	36	6	17	14	25	8	31	6	3	14	19			31	28
Furnarius minor	30				47	10	43	17		7	30	3	10		33
Synallaxis propinqua	34					9	91		3		56	9	24	9	
Cranioleuca vulpina	41	7	17	7	10	12	46	17	10	20	20			20	13
Thamnophilus cryptoleucus	47	4	15	21	23	21	15	26	9	43	4			15	3
Myrmotherula assimilis	12			17	33	50				75				17	8
Myrmoborus lugubris	22				86	14		55					23	22	
Myrmochanes hemileucus	75		3	7	31	17	43	1		9	13		5	63	8
Elaenia pelzelni	36	81	14	5				61	36	3					
Stigmatura napensis	19	11	5				84		11		79	10			
Serpophaga hypoleuca	15						100				20	80			
Cnemotriccus fuscatus	45	7	4	11	33	29	16	9	7	27	13		2	20	23
Conirostrum bicolor	44	86	14					61	36		2				
Conirostrum margaritae	10	90	10					100							
Nonobligate island species															
Chrysoptilus punctigula	21	29	19	24	5	10	14	33	43						24
Veniliornis passerinus	14	21	7	36	21	14		43	36		7				14
Synallaxis gujanensis	22				68	32		36		5				45	14
Synallaxis albigularis	29		3	3	17	24	52			10	10		45	38	7
Thamnophilus doliatus	11		18	9	9	27	36			27	36			18	19
Todirostrum maculatum	47	36	21	15	2	6	19	42	28	7	21			2	
Myiarchus ferox	13	62	15	23				46	31	15					8
Myiodynastes maculatus	23	43	35	13		9		70	17	13					
Tyrannus melancholicus	19	42	42				16	21	37		5	32			5
Tyrannus albogularis	21	52	24				24	29	48			14			9
Turdus ignobilis	39	69	18	5	8			82	8			5		5	
Thraupis episcopus	41	78	20	2				71	22			7			
Thlypopsis sordida	36	22	28	8	9	3	28	39	8	11	17	8		8	9
Ramphocelus carbo	14	29	64				7	79			14			7	
Sporophila castaneiventris	39	23	31	3			44	54	3		18	5	15		5
Saltator coerulescens	39	54	15		10	13	8	59	10	8	3			13	7
Ammodramus aurifrons	9					22	79				22	33	22		22

difficult to observe (e.g., species in the Ardeidae, Cathartidae, Accipitridae, Rallidae, Charadriidae, Columbidae, Psittacidae, Caprimulgidae, and Alcedinidae). Fourteen of these 110 species were determined to be obligate island species.

Five complete censuses on Tuhuayo yielded a total of 44 species (see Appendix for complete river-island species list), averaging 22.5 species (SD = 1.8) per visit. That only half the total number of species were detected per census suggest a high day to day turnover of migrating or roosting birds; this is consistent with other *Tessaria*-dominated habitats in southeastern Peru (Scott Robinson, pers. comm.). These "nonresidents" included several species that represented obvious wanderers from older islands (e.g., Pale-vented Pigeon, *Columba cayennensis,* Swallow-winged Puffbird, *Chelidoptera tenebrosa,* Great Kiskadee, *Pitangus sulphuratus,* Bicolored Conebill, *Conirostrum bicolor,* and Blue-gray Tanager, *Thraupis episcopus*). Counts of individuals averaged 108 (SD = 5.7) per visit. The 16 species present during all five censuses together exceeded 160 birds/ha. This amazingly high density is an order of magnitude greater than any published density figures for mature forest or secondary habitats in the tropics (Karr 1976), and illustrates how abundant birds on river islands can be. The

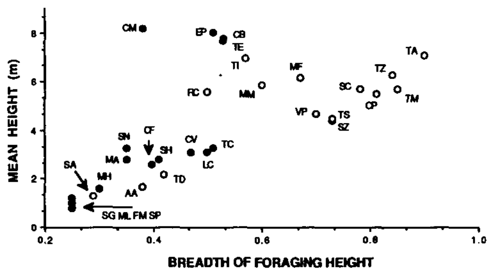

FIGURE 2. Niche breadths for microhabitat and plant species usage on the two study islands. The six categories for microhabitat are presented in Figure 1. The eight categories for plant species are listed in Table 4. Breadth values are presented as a proportion of the total number of categories for each variable (e.g., [actual breadth value/6] = value presented for breadth of microhabitat as there are six microhabitat categories). Shaded circles represent obligate island species and open circles represent nonobligate island species. See Table 5 for species abbreviations.

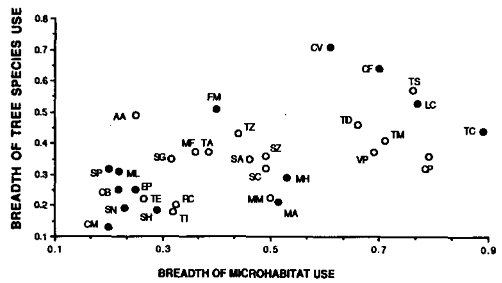

FIGURE 3. Mean foraging heights of river-island birds and niche breadths for foraging heights. Niche breadths are presented as a proportion of the total number of foraging heights (categories) available. Shaded circles represent obligate island species and open circles represent nonobligate island species. See Table 5 for species abbreviations.

most common resident on Tuhuayo was the White-bellied Spinetail (*Synallaxis propinqua*) with density estimates averaging about 20 individuals/visit (or about 47 birds/ha!).

HABITAT AND MICROHABITAT USE

Seven of the 14 obligate island species that I studied were specialized on a particular microhabitat (>75% of observations, Table 4). Of these Brown Elaenia, *Elaenia pelzelni,* and the two conebills, *Conirostrum bicolor* and *C. margaritae,* were restricted to the canopy of tall *Cecropia* forest. Pearly-breasted Conebill, *C. margaritae,* perhaps the least-known species in my study, was observed only near the tops of *Cecropia,* whereas the other two canopy species used *Mimosa* frequently. Three other specialists were restricted largely to sandbar scrub. White-bellied Spinetails and Lesser Wagtail-Tyrants, *Stigmatura napensis,* used *Tessaria* most heavily within the habitat, but the River Tyrannulet, *Serpophaga hypoleuca,* seemed to prefer the taller willows (*Salix*) when it foraged in the *Tessaria*-dominated scrub habitat. The Ash-breasted Antbird, *Myrmoborus lugubris,* was restricted to the understory of tall *Cecropia* forest.

The remaining obligate island species were not specialists; they occurred in more than one microhabitat. The Lesser Hornero, *Furnarius minor,* Leaden Antwren, *Myrmotherula assimilis,* and Black-and-white Antbird, *Myrmochanes hemileucus,* were primarily understory species. The Black-and-white Antbird was largely restricted to vine tangles, where it occasionally ascended along tree trunks into the middle story. The Leaden Antwren foraged mostly in the lower branches of the "broad-leafed" trees that grew primarily in the tall *Cecropia* forest. The Lesser Hornero foraged primarily on the ground in any habitat, and would occasionally be found off the ground on exposed roots or low branches.

In contrast, only two of the 17 nonobligate island species studied here were microhabitat specialists. Both are widespread tropical species; the Blue-gray Tanager, a canopy species, and the Yellow-browed Sparrow, *Ammodramus aurifrons,* a species of open, grassy, habitats both on and off islands. Four flycatchers, the Short-crested Flycatcher, *Myiarchus ferox,* the Streaked Flycatcher, *Myiodynastes maculatus,* the Tropical Kingbird, *Tyrannus melancholicus,* and the White-throated Kingbird, *T. albogularis,* as well as the Black-billed Thrush, *Turdus ignobilis,* and the Silver-beaked Tanager, *Ramphocelus carbo,* were all canopy specialists (when microhabitats 1 and 2 were combined); the two kingbird species also perched in the tops of willows in sandbar scrub habitat and occasionally flew between the two islands.

To summarize, a majority of the most specialized species, as illustrated by the breadth of microhabitat and tree-species use (Fig. 2), were obligate island species. Most of these were found almost exclusively in either *Cecropia* or *Tessaria* trees, and were either sandbar scrub or *Cecropia* forest specialists. However, some of the most generalized species with regard to these habitat

TABLE 5. Frequency of observations in various foraging technique and substrate categories used by 31 bird species on two river islands. n = sample size. Substrates include: LF = leaf; BK = bark; FR = fruit; GR = grass; GD = ground; FL = flower; and AR = air. Techniques include: GL = glean; SL = sally; HM = hammer; HV = hover; LG = lunge; and HG = hanging down. Species' codes are included after the name.

		Substrate							Technique					
Bird species	n	LF	BK	FR	GR	GD	FL	AR	GL	SL	HM	HV	LG	HG
Obligate island species														
Leucippus chlorocercus LC	16	19	6	6	6		63					100		
Furnarius minor FM	17		59			41	94				6			
Synallaxis propinqua SP	25	20	72		4			4	100					
Cranioleuca vulpina CV	30	37	63						93					7
Thamnophilus cryptoleucus TC	21	52	48						76	10			14	
Myrmotherula assimilis MA	9	67	33						89	11				
Myrmoborus lugubris ML	8	25	62			13			88				12	
Myrmochanes hemileucus MH	35	54	37		9				100					
Elaenia pelzelni EP	24	58		17				25	13	87				
Stigmatura napensis SN	16	94					6		38	50			12	
Serpophaga hypoleuca SH	11	82	18						18	82				
Cnemotriccus fuscatus CF	19	84	5		11					100				
Conirostrum bicolor CB	32	75	25						84	9				7
Conirostrum margaritae CM	8	88	12						87					13
Nonobligate island species														
Chrysoptilus punctigula CP	16		100						19		81			
Veniliornis passerinus VP	11		100								100			
Synallaxis gujanensis SG	7		71		14	15			100					
Synallaxis albigularis SA	8	25	63		12				100					
Thamnophilus doliatus TD	5	80	20						100					
Todirostrum maculatum TM	39	97	3						5	95				
Myiarchus ferox MF	7	86						14		100				
Myiodynastes maculatus MM	14	79	7					14		100				
Tyrannus melancholicus TZ	12	8						92		100				
Tyrannus albogularis TA	15	13		7				80		100				
Turdus ignobilis TI	19	5		95					26	74				
Thraupis episcopus TE	21	33	10	52				5	62	33			5	
Thlypopsis sordida TS	26	92	4	4					92	8				
Ramphocelus carbo RC	7	29	29	42					57	29				14
Sporophila castaneiventris SZ	10	10	30	10	50				100					
Saltator caerulescens SC	17	12	12	71				6	59	35				6
Ammodramus aurifrons AA	5		20		20			60	40	60				

variables were also obligate island species. These were all found in almost all the available microhabitat on the islands. Most nonobligate island species studied had intermediate breadth values for these measures.

FORAGING BEHAVIOR

Little was known about the foraging behavior of many species studied here, particularly those restricted to river-island habitats. Among the 14 obligate island species, 11 fed primarily in the understory within 3 m of the ground (Fig. 3), whereas the other three fed exclusively in the upper canopy. The mean foraging heights for the nonobligate island species were generally intermediate, with only four species found primarily in the understory vegetation. In addition to this difference in mean foraging height, obligate island species appeared to use a narrower range of heights than nonobligate island species as illustrated by their smaller niche breadths (Fig. 3).

In general, most river-island species were insectivorous, although some were at least partially frugivorous, taking advantage of the abundant supply of *Cecropia* fruit (Table 5). Among the obligate island species, only the Brown Elaenia fed to any extent on *Cecropia* fruit (4/4 stomachs contained *Cecropia* fruit). In contrast, seven of the nonobligate island species were considered specialized frugivores; the Black-billed Thrush mainly sallied out to pluck a piece of fruit, and then returned to a perch to eat it (1/1 stomach contained *Cecropia* fruit), whereas the Grayish Saltator, *Saltator caerulescens,* usually clung to a cluster of fruit from which it fed (no stomachs examined). In addition to the fruit specialists mentioned above (based upon foraging behavior), examination of stomachs from specimens collected on islands (LSUMNS tag data) revealed that the following species fed at least partially on *Cecropia* fruit: the Short-tailed Parrot, *Graydidasculus brachyurus* (8/8 stomachs); the Canary-winged Parakeet, *Brotogeris versicolorus* (4/8 stomachs); the Tui Parakeet, *B. sanctithomae,* (5/8 stomachs); the Blue-winged Parrotlet, *Forpus xanthopterygius* (4/4 stomachs); the Large Elaenia, *Elaenia spectabilis* (2/4 stomachs); the Small-billed Elaenia, *E. parvirostris* (2/2 stomachs); the Short-crested Flycatcher (1/4 stomachs); the Great Kiskadee (3/4 stomachs); the Streaked Flycatcher (1/1 stomach); the White-throated Kingbird (4/8 stomachs); the Hooded Tanager, *Nemosia pileata* (1/4 stomachs); and the Blue-gray Tanager (2/2 stomachs). *Cecropia* trees do not appear to be seasonal with regard to fruit production, with fruit present during visits in July, as well as January.

Among the obligate island species, most fed by either gleaning or sallying for insects on leaves or branches, with gleaners outnumbering salliers nine species to three. Of the understory species, only the Lesser Hornero and Ash-breasted Antbird were seen to feed on the ground. The hornero often foraged in clearings or in exposed sandy areas away from vegetation, whereas the antbird (along with the Plain-crowned Spinetail, *Synallaxis gujanensis*) often fed by moving about on exposed *Cecropia* roots occasionally dropping to the ground to search for insects. The Olive-spotted Hummingbird, *Leucippus chlorocercus,* was frequently seen hover-gleaning for insects at a variety of substrates. This is consistent with recent findings that most (if not all) tropical hummingbirds feed extensively on insects (Remsen et al. 1986). No obligate island species were exclusively bark-foragers, or sallied to any extent for aerial prey, except perhaps the Brown Elaenia (25% of the observations).

Nonobligate island species also mostly gleaned or sallied for insects, but, in contrast to obligate island species, there were as many sallying species as gleaners. Six species sallied for flying insects, with the two kingbird species specializing on that technique. The Spotted Tody-Flycatcher, *Todirostrum maculatum,* fed by sallying out to pick insects off the undersides of leaves, as do many of its congeners (Fitzpatrick 1976). Of the gleaners, the Dark-breasted Spinetail, *Synallaxis albigularis,* and the Plain-crowned Spinetail primarily search twigs and small branches, whereas the Barred Antshrike, *Thamnophilus doliatus,* and the Orange-headed Tanager, *Thlypopsis sordida,* searched mostly leaves. The Chestnut-bellied Seedeater, *Sporophila castaneiventris,* fed mostly on grass seeds, and the Yellow-browed Sparrow was seen "leaping" up into the air (a seemingly uncharacteristic behavior for an emberizid) for flying insects. The two woodpeckers both specialized by hammering for insects on trunks and branches.

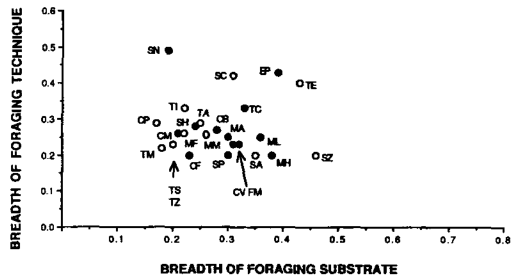

FIGURE 4. Niche breadth values based on foraging technique and foraging substrate. The six categories of techniques and seven categories of substrates are listed in Table 5. Breadth values are presented as a proportion of the total number of categories for each variable. Shaded circles represent obligate island species and open circles represent nonobligate island species. See Table 5 for species abbreviations.

Overall, there appeared to be no difference in the degree of foraging specialization between obligate and nonobligate island species, as illustrated by niche breadths for technique and substrate (Fig. 4). All species, however, were specialized in foraging technique and substrate.

DISCUSSION

The extreme geographic restriction exhibited by island birds in northeastern Peru represents a situation unique to the Amazon River and its tributaries. In no other tropical or temperate river basin in the world is such a high percentage of the avifauna dependent upon river-created habitats (Remsen and Parker 1983). If such a degree of river-created specialization were widespread, then, for example, an island in the Mis-

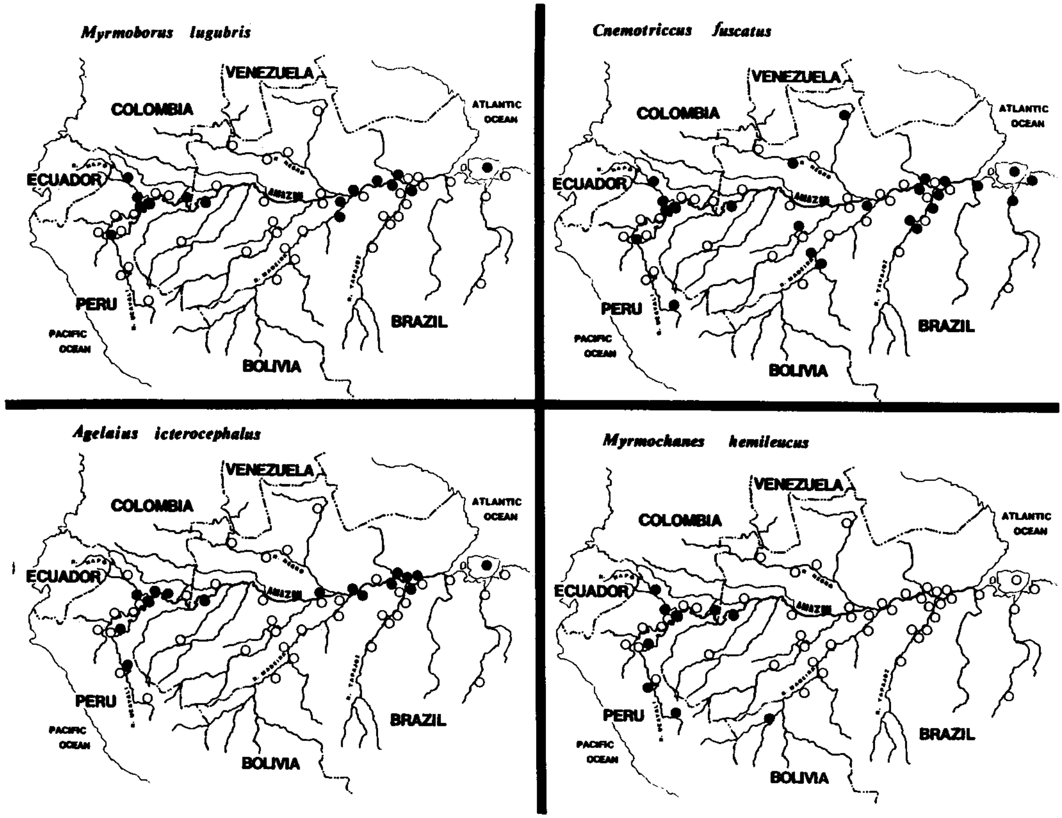

FIGURE 5. Distribution of four river-island bird species. Open circles represent all the collection localities for all river-island species combined based upon an extensive museum search. Shaded circles represent collecting localities at which specimens of that species were attained.

sissippi River would have 15–20 species present that were absent from the adjacent mainland deciduous forest (and absent from nonforested regions outside of the Mississippi drainage). What are the primary factors causing the habitat and geographic restriction found in northeastern Peru? Are bird species that are restricted to river islands in northeastern Peru restricted to islands throughout their range, or are they attracted to specific habitats that are found only on islands in this region of Amazonia?

Most obligate island species have widespread but linear distributions that fall into three categories (Fig. 5): (1) species found throughout Amazonia but restricted to the Amazon River and its largest tributaries, such as the Ucayali and Napo rivers (e.g., Ash-breasted Antbird, Yellow-hooded Blackbird, *Agelaius icterocephalus*, White-bellied Spinetail, and others); (2) like (1) but also found on most tributaries, large or small (e.g., Fuscous Flycatcher, *Cnemotriccus fuscatus*, Red-backed Spinetail, *Cranioleuca vulpina*, and Leaden Antwren); and (3) species restricted to western Amazonia along the Amazon, Napo, and Ucayali rivers (e.g., Black-and-white Antbird and Olive-spotted Hummingbird).

Away from northeastern Peru, several obligate island species have been found in similarly structured habitats away from islands. For example, in southeastern Peru, Terborgh and Weske (1969) found the River Tyrannulet in "matorral" habitat. Also, the Ash-breasted Antbird is known from river-edge forest on the mainland of Colombia, near Letecia, although the record represents only one sighting away from a river island in more than 10 months of fieldwork in *varzea* forest (J. V. Remsen, Jr., pers. comm.). Another pair was also recorded from *varzea* on the "mainland near Letecia in January 1984" (R. S. Ridgely, pers. comm.). The Fuscous Flycatcher occurs in *Tessaria*- and *Cecropia*-dominated second-growth, river-edge, and lake margins in southeastern Peru (T. A. Parker, III, pers. comm.). In addition, this species is found along sand ridges and in swampy forest in Suriname (Haverschmidt 1968). The Bicolored Conebill is found in coastal mangroves along the northern coast of South America (Haverschmidt 1968, Hilty and Brown 1986).

Evidence that island species may occasionally occur away from islands, even in western Amazonia, comes from a sandbar along the lower Napo that, in 1983, was covered with *Tessaria* scrub (later replaced by short *Cecropia* forest). All the bird species of *Tessaria* scrub were found on visits to this sandbar, even though it was connected to the mainland on one end. However, none was found in adjacent successional habitats along the mainland riverbank that lacked *Tessaria.* The formation of these sandbar peninsulas is apparently a rare phenomenon in northeastern Peru, but the presence of *Tessaria*-scrub birds there illustrates the likelihood that these obligate island species select particular habitats, rather than islands per se.

Given such habitat restriction, what features of this habitat were most important to the island birds? In general, little foraging-site specialization was apparent among island birds. This can be attributed to the simple structure of the vegetation (Terborgh 1980a), as well as to the lack of, or scarcity of many "novel" resources on the islands that contribute greatly to foraging-site specialization in mainland forests. These include: army ants (Willis and Oniki 1978); epiphytes (Orians 1969); suspended dead leaf clusters (Terborgh 1980b, Remsen and Parker 1984); and bamboo thickets (Parker and Parker 1982, Remsen 1985). However, the most important distinction between obligate and nonobligate island species was the specialization by obligate island species on understory and, in particular, *Tessaria*-scrub vegetation, which is largely absent from the mainland.

Specialization on these particular microhabitats poses special problems because they are ephemeral, and often completely under water during the high-water season (Remsen and Parker 1983). For species to take advantage of these habitats as they become available during the low-water season requires a degree of mobility and dispersal greater than what is considered usual for tropical understory birds (Diamond 1975). Several of the obligate island species belong to families (e.g., Formicariidae and Furnariidae) that are considered poor dispersers. Although virtually nothing is known about the dispersal capabilities of island species, the variety and abundance of birds recorded on Tuhuayo during my censuses, including several species not normally found in *Tessaria*-scrub habitat (e.g., Great Kiskadee, Black-billed Thrush, Bicolored Conebill, and Blue-gray Tanager), implies that many birds can disperse and find new islands, and that some may wander from island to island in search of their preferred habitat. Several species (e.g., both kingbirds, Chestnut-backed Oropendola, *Psarocolius angustifrons,* and Yellow-rumped Cacique, *Cacicus cela*) were regularly seen to fly between the mainland and the islands, and even roost on the islands. Amazingly, even a poor-flying terrestrial Undulated Tinamou, *Crypturellus undulatus,* has been seen to fly from the mainland to islands (J. V. Remsen, Jr. and R. S. Ridgely, pers. observ.).

Further anecdotal evidence of high dispersal capabilities in obligate island species comes from a visit to another small island in the Napo River in January 1989, which was less than 1 year old and partially covered with grass, and *Cecropia* and *Tessaria* saplings. The island was only about 200×75 m in size, and although I made only a short visit, I was able to determine that the White-bellied Spinetail was already "common" in the sparse vegetation. Other species present included the Ladder-tailed Nightjar, *Hydropsalis climacocerca,* the River Tyrannulet, the Chestnut-bellied Seedeater, and the Red-capped Cardinal, *Paroaria gularis.* Absent (despite playback of recorded song and calls in an attempt to determine presence or absence) were the following *Tessaria*-scrub species: the Black-and-white Antbird, the Lesser Wagtail-Tyrant, and the Riverside Tyrant, *Knipolegus orenocensis.*

In addition, almost nothing is known about the immediate responses of island species to the seasonal inundation of their habitat. In those extreme cases when entire islands are completely submerged, it is obvious that all the birds are forced to vacate the islands. However, during partial flooding, which most likely occurs on an annual basis, anecdotal evidence suggests that some species may leave the islands, while others appear to undergo vertical shifts depending on the height of the water. During a visit to a partially flooded young island, the White-bellied

Spinetail, normally abundant, was conspicuously absent, whereas the Lesser Hornero and the Dark-breasted Spinetail were both seen to feed uncharacteristically high in willow trees well above the water level (T. A. Parker, III, pers. comm.).

Equally important to the birds may be the consequences of natural succession of the island vegetation. As *Tessaria*-scrub vegetation gives way to *Cecropia*-dominated forest, many individuals must be forced to leave a particular island and search for a new home. Species found primarily in *Cecropia* forest encounter the same predicament as their preferred habitat gives way to older, more complex vegetation. Much more information on dispersal capabilities is needed before we can fully understand the temporal and spatial movements of obligate island birds.

The total area of river islands is certainly tiny relative to the Amazon basin as a whole, thus populations of obligate island species must be tiny relative to species of more widely distributed habitats (even though many of the island species are incredibly abundant). Furthermore, the existence of stable populations of several obligate island species depends on the continued formation and presence of new islands. Therefore, several of these species may be threatened by the higher flooding and increased erosion that may result from increased runoff attributed to deforestation in the Andes (Gentry and Lopez-Parodi 1980). Conservation plans for Amazonia should take into account this significant aspect of the avifauna and should protect river-created habitats, especially islands.

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APPENDIX

List of species that have been found on river islands along the Amazon and Napo rivers in northeastern Peru and southeastern Colombia. Data reflect information gathered by the LSUMNS, as well as the field experience of J. V. Remsen, Jr., Theodore A. Parker, III, and the author. Included is information on what age class of islands the species are found, on the type of habitat the species frequents on the mainland, on whether the species is a resident or visitor to the islands, on the relative abundance of the species on the islands, and on the foraging position when on the islands.

Island age (as described earlier). O = old; M = middle-aged; Y = young.

Mainland habitat. Fh = *terra firme* forest; Vz = *varzea* (seasonally flooded) forest; SH = secondary habitats including second-growth and man-influenced habitats; Rv = riverine habitats including river, stream, and lake margin, marsh, sandbar, and open water; + = all of the above. Note that a blank space in this column means that the species is not found on the mainland.

Island status. R = resident on the islands; V = visitor to the island but still a resident in this region of Amazonia; R-V = a portion of the population is resident but visitors from elsewhere occur as well; M = migrant from North America; Ma = austral migrant from southern South America.

Relative abundance. C = common (encountered daily); U = uncommon (encountered infrequently); R = rare (seen only occasionally but expected in proper habitat); X = accidental (seen fewer than three times, not expected).

Foraging position. 1 = canopy of old, tall, river-island forest; 2 = canopy of *Cecropia* forest; 3 = middle-story of old island forest; 4 = middle story of tall *Cecropia* forest; 5 = understory of old island forest; 6 = understory of *Cecropia* forest; 7 = *Tessaria* scrub; 8 = water-related habitats (riverbank, beach, open water); 9 = aerial habitats (including birds seen flying over islands).

Species	Island age	Mainland habitat	Island status	Relative abundance	Foraging position
Crypturellus undulatus	O, M	Ft	R–V	C	5, 6
Phalacrocorax olivaceus	O	Rv	V	R	8
Ardea cocoi	O, M	Rv	R	U	8
Casmerodius albus	O, M	Rv	R	U	8
Egretta thula	O, M	Rv	R	U	8
Hydranassa caerulea	O, M	Rv	R	R	8
Butorides striatus	O, M, Y	Rv	R	C	7, 8
Agamia agami	O	Rv	R	R	8
Pilherodius pileatus	O, M	Rv	R	U	8
Tigrisoma lineatum	O	Rv	R	R	8
Ixobrychus exilis	Y	Rv	R	R	8
Mesembrinibis cayennensis	O	Rv	R	R	8
Anhima cornuta	O, M, Y	Rv	R	U	5–8
Cairina moschata	O	Rv	V	X	8
Sarcoramphus papa	O, M, Y	+	V	R	9
Coragyps atratus	O, M, Y	+	V	C	9
Cathartes aura	O, M, Y	+	V	C	9
C. burrovianus	Y	Rv	V	R	9
C. melambrotus	O, M, Y	+	V	C	9
Elanoides forficatus	O, M, Y	+	V	U	9
Chondoheirax uncinatus	O	Rv	R	R	9
Ictinia plumbea	O	+	R	C	9
Rostrhamus sociabilis	O	Rv	R	R	8, 9
Helicolestes hamatus	O	Rv	R	R	8, 9
Buteo albonotatus	O, M	+	V	R	9
B. magnirostris	M, Y	SH	R	C	2, 4, 9
Busarellus nigricollis	O	Rv	R	U	8, 9
Buteogallus urubitinga	O	Ft	R	U	1, 3, 8, 9
Spizastur melanoleucus	O	?	V	X	9
Spizaetus tyrannus	O	Vz	V	X	9
Geranospiza caerulescens	O	Rv	R	R	1, 3, 9
Pandion haliaetus	O, M, Y	Rv	V	R	8, 9
Herpetotheres cachinans	O, M	Rv	R–V	U	1, 2, 9
Daptius ater	O	Rv	V	C	8, 9
Milvago chimachima	M, Y	Rv, SH	R–V	C	8, 9
Falco rufigularis	O	Rv	V	U	1, 9
Ortalis guttata	O	Rv	R	U	1, 3, 8
Opisthocomus hoazin	O	Rv	R	U	3, 8
Aramides cayanae	O	Vz, Rv	R	U	5, 8

APPENDIX. Continued.

Species	Island age	Mainland habitat	Island status	Relative abundance	Foraging position
Laterallus fasciatus	O	Vz, SH	R	R	5
Porphyrula martinica	Y	Rv	R	U	8
P. flavirostris	O	Rv	R?	R	8
Heliornis fulica	O	Rv	R	R	8
Jacana jacana	O	Rv	R	C	8
Hoploxypterus cayanus	Y	Rv	R–V	U	8
Charadrius collaris	Y	Rv	R–V	U	8
Tringa solitaria	O, M, Y	Rv	M	U	8
T. flavipes	O, M, Y	Rv	M	U	8
T. melanoleuca	O, M, Y	Rv	M	U	8
Actitis macularia	O, M, Y	Rv	M	U	8
Calidris fuscicollis	O, M, Y	Rv	M	X	8
C. melanotis	O, M, Y	Rv	M	U	8
Phaetusa simplex	O, M, Y	Rv	R–V	C	8
Sterna superciliaris	O, M, Y	Rv	R–V	C	8
Rynchops niger	Y	Rv	R–V	U	8
Columba cayennensis	O, M, Y	Rv, SH	R–V	C	1, 2, 7
C. subvinacea	O, M	Vz	V	X	1, 2
Columbina talpacoti	M, Y	Rv, SH	R	C	6, 7
Leptotila verreauxi	M	SH	R	U	6
L. rufaxilla	O, M	SH	R	U	5, 6
Ara ararauna	O, M, Y	+	V	R	9
A. macao	O, M	+	V	R	9
A. chloroptera	O	+	V	R	9
A. serva	O, M	Rv	R	U	1, 2, 9
A. manilata	O	Rv	R	U	1, 9
Aratinga leucophthalmus	O, M	Vz	R	C	1–4, 9
A. weddellii	O	Vz	R	U	1, 3, 9
Forpus xanthopterygius	M	XX	R	U	5, 9
Brotogeris versicolorus	O, M	Rv	R	C	1–4
B. cyanopterus	O, M	Rh, Vz, SH	R	C	1–4, 7, 9
B. sanctithomae	O, M	Fh, Rv, SH	R	C	1–4, 9
Graydidasculus brachyurus	O, M	Vz, Rv	R	C	1, 2, 9
Pionus menstruus	O	Vz, Rv, SH	R	C	1, 9
Amazona festiva	O	?	R	U	1, 9
A. ochrocephala	O	+	V	R	1, 9
A. amazonica	O, M	Vz, Rv	R	C	1, 2, 9
Coccyzus americana	O	?	M	X	1
C. melacoryphus	O, M, Y	SH	R	U	1–7
Piaya minuta	M	SH	R	U	4, 6
Crotophaga major	O	Vz, Rv	R	U	3, 8
C. ani	O, M, Y	Rv, SH	R	C	3–7
Tapera naevia	M	Rv, SH	R	U	6, 7
Otus choliba	O	Vz, SH	R	C	1, 3
Glaucidium brasilianum	M	Vz, SH	R	U	2, 4
Rhinoptynx clamator	M, Y	?	R	R	6, 7
Nyctibius griseus	O	Vz, Rv	V	R	1
Chordeiles rupestris	Y	Rv	V	C	7, 8, 9
C. minor	O, M, Y	Rv	M	R	9
Nyctidromus albicollis	O, M, Y	SH	R	C	5, 6, 7
Hydropsalis climacocerca	Y	Rv	R	C	7
Podager nacunda	O	?	V	X	9
Caprimulgus parvulus	Y	?	V	X	7
Chaetura cinerieventris	O, M, Y	+	V	U	9
C. brachyura	O, M, Y	+	V	C	9
Panyptila cayennensis	O, M, Y	+	V	R	9
Reinarda squamata	O, M, Y	+	V	C	9
Glaucis hirsuta	O, M	Vz	R	C	5, 6
Phaethornis hispidus	O, M	Vz	R	C	5, 6
Campylopterus largipennis	O	Vz, SH	R	U	1, 3

APPENDIX. Continued.

Species	Island age	Mainland habitat	Island status	Relative abundance	Foraging position
Florisuga mellivora	M	Fh, Vz, SH	R	C	2, 4
Anthracothorax nigricollis	M, Y	Vz	R	U	2, 4, 7
Lophornis chalybea	O, M	?	R	R	1, 2
Chlorestes notatus	O, M	?	R	U	3–6
Chlorostilbon mellisugus	M	?	R	U	4, 6
Leucippus chlorocercus	M, Y		R	C	4, 6, 7
Amazilia fimbriata	M	SH	R	C	4, 6
A. lactea	O	SH	R	R	?
Heliomaster longirostris	O, M	SH	R	U	1, 2
Ceryle torquata	O, M	Rv	R	C	8
Chloroceryle amazona	O, M	Rv	R	C	8
C. americana	O, M	Rv	R	C	8
C. aenea	O, M	Rv	R	U	5–8
Galbalcyrhynchus leucotis	O	Vz, Rv, SH	R	C	1, 3
Monasa nigrifrons	O	Vz, SH	R	C	1, 3
Capito aurivirens	O, M	Vz	R	U	1–4
Pteroglossus castanotis	O, M	Vz	R	C	1–4
Picumnus castelnau	O, M		R	R	3, 4
Chrysoptilus punctigula	O, M	SH	R	U	3, 4
Celeus elegans	O	Fh, Vz	R	R	3
C. flavus	O	Vz	R	U	1, 3
Dryocopus lineatus	O, M	Vz, SH	R	R	1–4
Melanerpes cruentatus	O	SH	R	U	3
Veniliornis passerinus	O, M	SH	R	U	3, 4
Campephilus melanoleucus	O	Vz	R	R	1, 3
Nasica longirostris	O	Vz	R	R	1, 3
Dendrexetastes rufigula	O, M	Vz	R	U	1–4
Xiphorhynchus picus	O, M	Vz, SH	R	U	3, 4
Furnarius torridus	O, M		R	U	5, 6
F. minor	M, Y		R	C	6, 7
Synallaxis albescens	O	SH	M	X	5
S. albigularis	M, Y	SH	R	C	6, 7
S. gujanensis	O, M	SH	R	C	5, 6
S. propinqua	M, Y		R	C	6, 7
Cranioleuca vulpina	M, Y		R	C	6, 7
Certhiaxis cinnamomea	O		R	R	8
C. mustelina	O		R	R	8
Metropothrix aurantiacus	M	SH	R	R	6
Taraba major	O	SH	R	U	5
Thamnophilus doliatus	M, Y	SH	R	U	6, 7
T. cryptoleucus	O, M		R	C	4, 6
Myrmotherula assimilis	O, M		R	U	3–6
Cercomacra nigrescens	O, M	SH	R	U	5, 6
Myrmoborus lugubris	O, M		R	C	5, 6
Myrmochanes hemileucus	M, Y		R	C	6, 7
Cotinga maynana	O	Vz, Rv	R	U	1
Gymnoderus foetidus	O	Vz, Rv	R	U	1
Cephalopterus ornatus	O	Vz, Rv	R–V	R	1
Schiffornis major	O	Vz, Rv	R	C	5
Camptostoma obsoletum	M	SH	R	U	2, 4
Tyrannulus elatus	O	Vz, Rv	R	U	1
Sublegatus arenarum	M	?	R	R	6
Elaenia spectabilis	M		Ma	U	2, 4
E. pelzelni	M		Ma	U	2, 4
E. parvirostris	M, Y		Ma	R	4, 6, 7
Serpophaga hypoleuca	Y		R	U	7
Stigmatura napensis	Y		R	U	7
Todirostrum latirostre	M	SH	R	U	6
T. maculatum	O, M, Y	SH	R	C	3, 4, 7
Tolmomyias flaviventris	M	SH	R	U	4

APPENDIX. Continued.

Species	Island age	Mainland habitat	Island status	Relative abundance	Foraging position
Myiophobus fasciatus	M, Y	SH	R	R	6, 7
Cnemotriccus fuscatus	M, Y		R	C	4, 6, 7
Pyracephalus rubinus	M, Y	SH	R	R	6, 7
Ochthornis littoralis	O, M, Y	Rv	R	C	8
Muscisaxicola fluviatilis	Y		V	U	8
Knipolegus orenocensis	Y		R	R	7, 8
Fluvicola leucocephala	Y	Rv	R	C	7, 8
Attila cinnamomeus	O	Vz, Rv	R	R	1, 3
A. bolivianus	O	Vz	R	R	1, 3
Myiarchus ferox	M	SH	R	C	4
M. swainsoni	O	Fh, Vz	Ma	X	3
Pitangus sulphuratus	O, M, Y	Rv, SH	R–V	C	1–7
P. lictor	O	Rv	R	U	8
Megarynchus pitangua	M	Vz, SH	R	C	2, 4
Myiozetetes similis	M, Y	SH	R	C	2, 4, 6, 7
M. granadensis	M	SH	R	U	2, 4
Myiodynastes maculatus	O, M	SH	R	C	2, 3, 4
Empidonomus varius	O	Fh, Vz	Ma	X	1
Tyrannus albogularis	M, Y	Rv	Ma	U	2, 7, 8
T. melancholicus	O, M, Y	+	R–M?	C	1–9
T. savana	O, M	SH	Ma	U	2, 8
T. tyrannus	O	+	M	R	1
Pachyramphus rufus	M		R	R	2, 4
P. castaneus	M	Vz, SH	R	R	2, 4
P. polychopterus	M	Vz, SH	R	C	2, 4
Tityra cayana	O, M	Fh, Vz	R	R	1, 2
T. inquisitor	O	Vz	V	X	1
Tachycineta albiventer	O, M, Y	Rv	V	C	8, 9
Progne chalybea	O	Rv	V	X	9
P. tapera	M, Y	Rv	R–V	R	8, 9
Atticora fasciata	O	Rv	V	R	9
Stelgidopteryx ruficollis	O	Rv	R–V	C	8
Riparia riparia	O, M, Y	Rv	M	C	8, 9
Hirundo rustica	O	Rv	M	X	9
Petrochelidon pyrrhonota	O	Rv	M	X	9
Cyanocorax violaceus	O, M	Vz, SH	R	R	1, 2
Campylorhynchus turdinus	O	Vz, SH	R	U	3
Thryothorus leucotis	O, M	Vz, SH	R	C	5, 6
Donacobius atricapillus	O, M, Y	Rv	R	C	8
Turdus ignobilis	O, M, Y	SH	R	C	1–7
Vireo olivaceus	O, M	Vz, SH	R	C	1, 2
Molothrus bonariensis	M, Y	Rv	R	C	2, 7, 8
Scaphidura oryzivora	Y	Rv, SH	V	R	7, 8
Ocyalis latirostris	O	Vz	V	X	1
Psarocolius decumanus	O	Vz	R	U	1
P. angustifrons	O, M	Vz, SH	R	C	1, 2
Cacicus cela	O, M	Fh, Vz, SH	R	C	1, 2
C. solitarius	O, M	SH	R	R	5, 6
Lampropsar tanagrina	O	Vz	R	R	1, 3, 5
Agelaius icterocephalus	Y	Rv	R	C	8
Icterus icterus	O, M, Y	SH	R	U	1–7
Gymnomystax mexicanus	M, Y	Rv	R	C	2, 4, 7, 8
Dendroica striata	M, Y	SH	M	R	2, 4, 7
Conirostrum bicolor	M, Y		R	R	2, 7
C. margaritae	M		R	R	2
Euphonia laniirostris	O, M	SH	R	R	1, 2
Thraupis episcopus	O, M, Y	SH	R	C	1, 2, 7
T. palmarum	O, M	SH	R	U	1, 2
Ramphocelus carbo	O, M	SH	R	C	3, 4, 6
R. nigrogularis	O	Vz, Rv, SH	R	U	3, 5

APPENDIX. Continued.

Species	Island age	Mainland habitat	Island status	Relative abundance	Foraging position
Nemosia pileata	O, M	Rv, SH	R	U	1, 2
Thlypopsis sordida	O, M, Y	Rv, SH	R	C	1–7
Eucometis penicillata	O	Vz	R	R	5
Cissopis leveriana	M	SH	R	U	2
Saltator caerulescens	O, M	SH	R	C	1–4, 7
Paroaria gularis	O, M, Y	Rv, SH	R	C	1–7
Sporophila americana	O, M, Y	Rv, SH	R	C	6, 7, 8
S. lineola	O, Y	Rv	V	U	7, 8
S. castaneoventris	O, M, Y	Rv, SH	R	C	6, 7, 8
Oryzoborus angolensis	M	SH	R	R	6
Ammodramus aurifrons	O, M, Y	Rv, SH	R	C	6, 7, 8