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BROMELIAD FORAGING SPECIALIZATION AND DIET SELECTION OF *PSEUDOCOLAPTES LAWRENCII* (FURNARIIDAE)

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ABSTRACT.—Over 50 species of Neotropical birds have been recorded foraging for animal prey in bromeliads. Of these bird species, *Pseudocolaptes lawrencii* is one of the most specialized. At a montane rainforest site in Costa Rica, 74% of its documented foraging efforts were in epiphytic bromeliads. *P. lawrencii* selected large bromeliads and foraged for arthropods within leaf litter and organic debris trapped in the plants. Based on our analyses of the bromeliad prey base and bird stomach contents, *P. lawrencii* was an opportunistic predator of the litter-inhabiting arthropods. Birds consumed dermapterans, orthopterans, arachnids, and coleopterans in proportions equal to the prey's availability and did not select for prey size. However, *P. lawrencii* avoided isopods. *P. lawrencii* did not consume aquatic insect larvae, which were the largest component of the bromeliad prey base and occurred in 80% of bromeliads sampled.

RESUMEN.—Mas de 50 especies de aves Neotropicales han sido estudiadas mientras forrajean por animales en bromelias. De estas especies de aves, *Pseudocolaptes lawrencii* es una de las mas especializadas. En un bosque tropical montañoso en Costa Rica, se encontró que el 74% de los atentos de forrajeo fueron en bromelias epifiticas. *Pseudocolaptes lawrencii* selecciono bromelias grandes y forrajeo en las hojas y los escombros orgánicos atrapados en las bromelias. Basado en nuestro análisis de los animales encontrados en las bromelias y el contenido estomacal de las aves, concluimos que *P. lawrencii* es un predador oportunistico de los artrópodos que viven en los escombros orgánicos. Las aves consumieron dermapteros, orthopteros, aracnidos y coleopteros en proporciones idénticas a la disponibilidad de estas presas. No se encontró selección de presas, sin embargo, *P. lawrencii* evito isopodos. No consumió larvas de insectos acuáticos, la presa mas abundante y se encontró en un 80% de las bromelias estudiadas.

Among the masses of epiphytes that give Neotropical montane forests their "fantastic appearance" (Slud 1964:205), bromeliads are often the most conspicuous plants. Bromeliads increase the structural complexity of forests and create additional microhabitats for birds and their animal prey. Indeed, a diverse fauna exists within the impounded water and detritus of tank bromeliads (e.g., Picado 1911, Pittendrigh 1948, Laessle 1961, Diesel 1989, Paoletti et al. 1991), consisting of two primary components: animals living within the aquatic medium (e.g. dipteran larvae, frogs) and animals typically associated with soil and organic debris (e.g., earwigs [Dermaptera], roaches [Orthoptera], isopods). Thus, bromeliads can enhance opportunities for resource subdivision and specialization by birds in Neotropical forests. Foraging specialization on unique tropical resources, such as bromeliads, is thought to be one mechanism responsible for the high bird species diversity of the Neotropics relative to the Temperate Zone (Schoener 1968; Orians 1969; Karr 1971; Terborgh 1980; Remsen 1985). At least 51 Neotropical bird species have been recorded foraging for animal prey in bromeliads (Appendix). Nine species appear to be specialized on bromeliad foraging; most of these belong to the Dendrocolaptidae and Furnariidae.

Tuftedcheeks (Furnariidae: *Pseudocolaptes lawrencii*, *P. boissonneautii*, and *P. johsoni*) are

among the most specialized of bromeliad-foraging birds. They occur in wet montane forests of southern Central America and the Andes (Slud 1964; Hilty and Brown 1986; Fjeldså and Krabbe 1990; Ridgely and Tudor 1994; Sillett 1994). At a montane rainforest site in Costa Rica, 74% of foraging observations of *P. lawrencii* were in arboreal bromeliads, and nearly 99% of its foraging efforts were in epiphytes of one type or another (Sillett 1994).

In this paper, we present further data on the natural history and foraging ecology of *P. lawrencii.* We focus on the bird's use of and selectivity for the bromeliad resource base to determine if the bird specializes on particular prey types, prey sizes, and bromeliad sizes. The null hypothesis we test is that *P. lawrencii* uses bromeliad resources in proportion to their availability.

STUDY AREA AND METHODS

Our research was conducted in the Cordillera de Talamanca, Costa Rica, near Villa Mills and the Pensión La Georgina (83°40′W longitude, 9°30′N latitude; hereafter "La Georgina"), approximately 95 km south of San José along the Pan American Highway. All data were collected from 3 July to 11 August 1991. We worked in a 4-km^2 area of montane rainforest (Holdridge 1967) between 2,800 and 3,100 m elevation, near the transition zone from oak forest to páramo vegetation. Trees are covered with diverse epiphytic vegetation, including bryophytes, lichens, and tank bromeliads (species of *Guzmania, Vriesea,* and *Tillandsia* [Burt-Utley and Utley 1977]). *Quercus costaricensis* is the dominant canopy tree. A more complete description of the study site is given by Sillett (1994).

To compare *P. lawrencii's* selection of bromeliad sizes to the bromeliad size distribution available at La Georgina, we collected foraging observations and conducted vegetation surveys. Foraging data were gathered on opportunistically encountered birds. We took only one observation per individual bird per day to minimize sequential observations and to avoid serial correlation problems (Martin and Bateson 1986; Hejl et al. 1990). Bromeliad size (diameter across the top of each plant's rosette of leaves) was estimated for every bromeliad in which *P. lawrencii* was observed foraging. To quantify the available bromeliad size distribution, we randomly selected 120 points in the oak forest at La Georgina. At each point, imaginary 1-m diameter cylinders were delineated, extending from ground to forest canopy. We estimated sizes of all bromeliads encompassed by the cylinders. Bromeliads were classified into three size categories before data analyses: small (1–30 cm), medium (31–60 cm), and large (>60 cm). More detailed descriptions of methods used to gather foraging and vegetation data are given in Sillett (1994).

Ten foraging *P. lawrencii* were collected with shotguns in the vicinity of La Georgina for analysis of stomach contents. Birds were prepared as either study skins or skeletons; tissue samples from each bird were preserved in liquid nitrogen. Stomach samples were preserved in 70% ethanol as soon as possible after collection. All specimens, as well as tissue and stomach samples, were deposited in the Louisiana State University Museum of Natural Science. Stomach contents were sorted and identified to Class or Order under a dissecting microscope. Minimum numbers of prey items in each category were determined from diagnostic fragments (e.g. mouthparts, heads, and wings). Arthropod fragments were identified using illustrations in Ralph et al. (1985), Moreby (1987), Borer et al. (1989), and Chapman and Rosenberg (1991), and then measured with the microscope's optical micrometer. Fragment size was converted to prey size using regression equations in Calver and Wooller (1982), K. V. Rosenberg (unpublished data), and an equation determined for Dermaptera in the present study (body length = $0 + 3.02 \times$ [cercus length]; $R^2 = 0.93$; 20 animals measured). We believe that with knowledge of the particular fragments representing different types of arthropods, we were able to detect hard-bodied and soft-bodied prey equally well. However, the potential biases associated with differential digestion of hard-versus soft-bodied prey are poorly understood (Rosenberg and Cooper 1990 and references therein).

We collected 45 tank bromeliads from randomly selected locations in the study site to quantify the bromeliad prey base. All bromeliads collected were attached to trees and within 2.5 m of the ground. To quantify the bromeliad prey base encountered by foraging *P. lawrencii,* we sampled a size distribution of bromeliads comparable to the size distribution selected by the bird. Bromeliads were placed in plastic bags immediately upon collection to minimize escape of arthropods. Before sealing the bags, a small amount of insecticide was sprayed inside to kill any flying insects. We opened bags in a large wash tub within 24 hr of collection and measured each bromeliad across the top of the rosette of leaves. We then carefully dissected the bromeliads, collected all animals encountered and preserved them in 70% ethanol. Arthropods were identified to Class or Order and measured under a dissecting microscope. Insect larvae were classified as

either terrestrial (larvae found in impounded dry leaf litter and detritus, most of which were Coleoptera and Lepidoptera) or aquatic (larvae found in impounded water and wet detritus, primarily Diptera, e.g., Syrphidae, Ceratopogonidae).

We used the Brillouin diversity index, H (Hurtubia 1973; Pielou 1975; Sherry 1984), to assess if our samples of *P. lawrencii* stomachs and bromeliad contents adequately represented the diversity of prey types consumed by the bird and available at La Georgina.

$$H = \left(\frac{1}{P}\right) \times \ln\left(\frac{P!}{(p_1! \times p_2! \times \ldots \times p_n!)}\right)$$

where there are p prey items in each of n different prey categories, with P total prey items per sample (Pielou 1975). To calculate H, samples were taken in random order, and the diversity of prey items was computed for sample 1, then for samples 1 + 2 (contents pooled), and so on through the total number of stomach or bromeliad samples. The saturation curves generated by these calculations become asymptotic if enough samples exist to characterize prey composition (Sherry 1984).

We conducted a series of statistical tests to measure specialization by *P. lawrencii* on bromeliad resources. Statistics were calculated using JMP (SAS Institute 1994). The null hypothesis for all tests was that use of bromeliad resources by *P. lawrencii* equaled resource availability. We considered the bird to specialize on, or be selective of, a resource when use was significantly greater than availability by 10%. A resource was classified as avoided by *P. lawrencii* when use was significantly less than availability by 10%. We tested for a difference between selection of bromeliad size classes by *P. lawrencii* and available size classes at La Georgina with a Pearson χ^2 test. Multiple analysis of variance (MANOVA) was used to test first for an overall difference between bird diet and available bromeliad-inhabiting prey, comparing prey composition and prey size. Four prey types (i.e. Dermaptera, Orthoptera, Arachnida, and Coleoptera) were sufficiently common in both stomachs and bromeliad samples to use in assessing prey size-selectivity by *P. lawrencii*. Bird use of individual prey types was compared to those available in La Georgina bromeliads with one-way analyses of variance (ANOVA). Individual bird stomachs and bromeliad samples were treated as replicates, and proportion data were arcsine-transformed before statistical analysis. Homogeneity of treatment variances (i.e. "used" by *P. lawrencii* and "available" in bromeliads) was assessed with Levene's test (Milliken and Johnson 1984). We used Welch's ANOVA (Welch 1951; Milliken and Johnson 1984) when treatment variances were heterogeneous.

RESULTS

Diversity of available prey generally increased with increasing bromeliad size (Fig. 1), as did mean number of prey per bromeliad (Welch ANOVA, $F_{2, 11.49} = 15.25$, $P = 0.0006$). Mean prey size, however, did not change with bromeliad size (ANOVA, $F_{2, 67} = 0.0046$, $P = 0.99$). Prey-type diversity saturation-curves became asymptotic for stomachs of *P. lawrencii* and medium and large bromeliads (Fig. 1). Therefore, our samples were adequate to characterize the range of prey items consumed by *P. lawrencii* and available at La Georgina, given the level of taxonomic resolution used in this study.

Use of bromeliad size classes by *P. lawrencii* differed from the available size distribution at La Georgina ($\chi^2_2 = 19.51$, $P = 0.0001$). The birds avoided small bromeliads (≤30 cm diameter) and specialized on the largest size class (<60 cm diameter, Fig. 2). Although we did not quantify sequential foraging behavior and substrate selection of individual *P. lawrencii*, we typically observed birds moving deliberately among large bromeliads and ignoring most small plants as they foraged. The size distribution of the 45 bromeliads collected for prey base analysis did not differ from use of bromeliad sizes by *P. lawrencii* ($\chi^2_2 = 2.84$, $P = 0.24$).

Proportional use of all prey types by *P. lawrencii* differed from prey availability (MANOVA, Wilks' $\lambda = 0.43$, $F_{9, 45} = 6.51$, $P < 0.0001$). In contrast, mean sizes of prey types consumed by *P. lawrencii* did not differ from available prey sizes (MANOVA, Wilks' $\lambda = 0.80$, $F_{3, 14} = 1.15$, $P = 0.36$). *Pseudocolaptes lawrencii* primarily fed on dermapterans, orthopterans (mainly roaches), coleopterans, and insect egg cases (Fig. 3). Nearly all egg cases in stomachs of *P. lawrencii* were from roaches. We considered insect egg cases to be a separate prey type because stomachs of several other species of epiphyte-searching insectivorous birds at La Georgina contained roach egg cases without any evidence that the birds consumed roaches (Sillett 1994). However, less than five percent of documented foraging observations of these species were in bromeliads (Sillett 1994). In addition, only a small fraction of roaches collected from bromeliads were

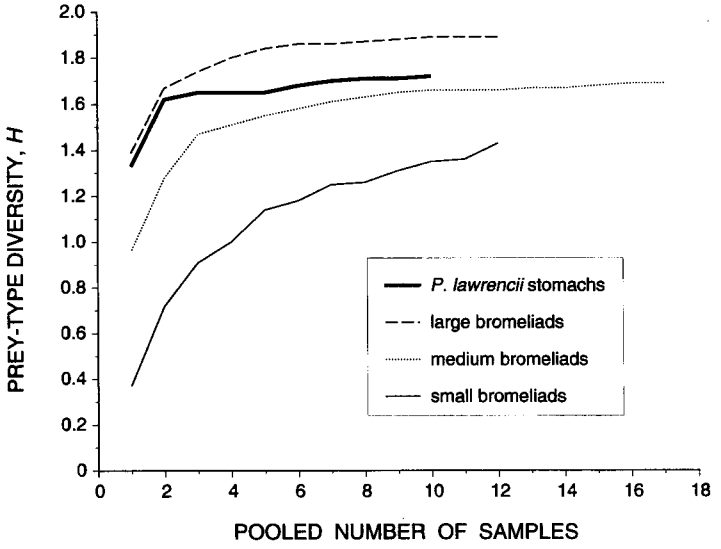

FIG. 1. Brillouin diversity saturation curves as a function of number of samples examined. Curves were produced by randomly sampling bromeliad and stomach data, with replacement.

carrying egg cases (personal observations). We concluded that *P. lawrencii* probably obtains most egg cases from substrates other than bromeliads, such as mats of epiphytic bryophytes (see Sillett 1994), and therefore did not include insect egg cases in further analyses.

Aquatic insect larvae were the largest component of the bromeliad prey base, and occurred in 80% of bromeliads sampled; yet, *P. lawrencii* did not use this resource, based on stomach contents (Fig. 3). Aquatic insect larvae, especially dipterans, have few sclerotized body parts and thus might be underrepresented in stomach samples. However, we have additional evidence suggesting that *P. lawrencii* did not feed on aquatic larvae. First, while in bromeliads, *P. lawrencii* primarily forages in leaf-litter trapped among the plants' outer leaves. One can usually find the birds by listening for their noisy rummaging in bromeliads and then by looking for the falling leaves and detritus tossed out as they forage. We never saw *P. lawrencii* visibly foraging in impounded water. Second, none of the 10 specimens we collected had wet or soiled feathers around the face, throat, or breast that would have been expected if the birds were foraging in water and wet debris.

We concluded that only terrestrial bromeliad-inhabiting prey were available to *P. lawrencii* at La Georgina, and removed all aquatic animals from further analyses. Considering only terrestrial

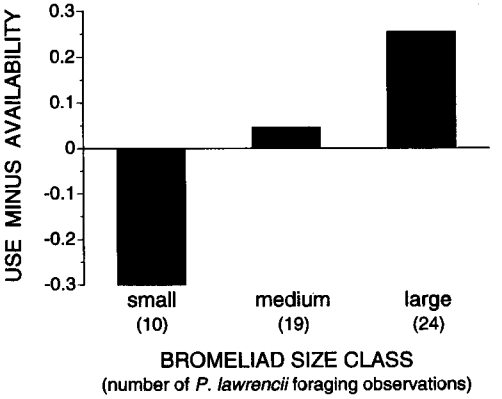

FIG. 2. Use of bromeliad size classes by *P. lawrencii* compared to available bromeliad sizes. Bars above 0.0 horizontal axis indicate selection; bars below indicate avoidance.

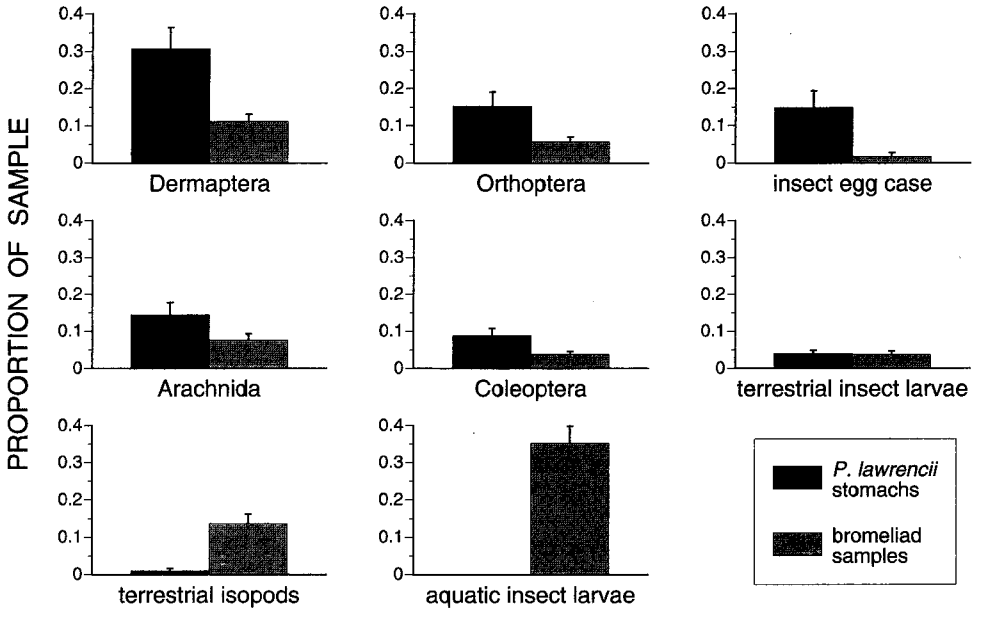

FIG. 3. Comparison of mean proportions of nine prey types in the diet of *P. lawrencii* with the bromeliad prey base. Error bars represent one standard error of mean.

prey, the bird's proportional use of prey types still differed from prey availability (MANOVA, Wilks' $\lambda = 0.69$, $F_{7, 40} = 2.52$, $P = 0.03$). With the exception of isopods, however, which were avoided by *P. lawrencii*, use did not differ from availability for all other prey types (Table 1).

DISCUSSION

The avoidance of isopods by *P. lawrencii* suggests that these crustaceans may be difficult to catch or unpalatable to the bird. The former explanation is unlikely because bromeliad-inhabiting isopods at La Georgina are not fast-moving (personal observations). Isopods are frequently consumed by some land and aquatic bird species (e.g., Weller 1975; Reinecke 1979; Sakai et al. 1986). However, isopods are dorsoventrally flattened and covered by a heavy, calcified exoskeleton (Siefert 1961 as cited in Graveland and Van Gijzen 1994). They may thus present less of an energy reward to *P. lawrencii*, relative to bromeliad-inhabiting insects, causing the birds to spend the majority of their foraging efforts on more profitable prey. A third explanation for the absence of isopods in the diet of *P. lawrencii* is that isopods are not prevalent in canopy bromeliads at La Georgina. Nadkarni and Longino (1990) documented significantly fewer crus-

TABLE 1

RESULTS OF ANOVAS COMPARING PROPORTIONAL USE OF EIGHT PREY TYPES BY *P. lawrencii* TO PREY AVAILABILITY IN LA GEORGINA BROMELIADS

Prey type	DF[a]	*F*	*P*-value	Power[b]
Dermaptera	1, 46	3.00	0.09	0.92
Orthoptera	1, 46	2.01	0.16	0.99
Arachnida	1, 46	0.02	0.90	0.97
Coleoptera	1, 46	0.02	0.89	0.84
Terrestrial insect larvae	1, 45.99	2.10[c]	0.15	1.00
Terrestrial isopods	1, 38.14	21.29[c]	<0.0001	—

[a] DF = degrees of freedom.

[b] Statistical power ($1 - \beta$) is given for all tests that failed to reject the null hypothesis that *P. lawrencii* use of prey did not differ from prey availability. Power was computed as the probability of an ANOVA to detect an actual difference (δ) of 10% between use and availability (i.e. $\delta = 0.1$) at the $\alpha = 0.05$ level.

[c] Welch ANOVA (see Methods).

taceans (isopods and amphipods) in canopy organic matter relative to the forest floor in a Costa Rican cloud forest. All of our bromeliad samples were collected within 2.5 m of the ground.

Pseudocolaptes lawrencii is highly stereotyped in its foraging behavior and selection of foraging substrates (Sillett 1994). This stereotypy may explain why *P. lawrencii* rarely consumes aquatic prey. Searching for prey in detritus-filled water probably requires different behaviors than foraging in drier, impounded leaf litter and organic matter. Leaf litter-inhabiting insects and spiders with an active predator-avoidance response would quickly move to seek cover if suddenly exposed by a rummaging bird. Such mobile prey would be rapidly detected by an actively foraging bird. In contrast, *P. lawrencii* could not easily remove impounded water to expose aquatic prey, given the bird's pointed and relatively stout bill. Water collects in the bases of bromeliad leaf axils and occurs at a greater depth in the center of plants, where leaves are younger, denser, and more erect (Laessle 1962). The majority of aquatic animals we sampled occurred toward bromeliad centers. It may be more difficult for *P. lawrencii* to probe and rummage among dense, young leaves than in more widely spread, older leaves.

Little is known about what components of the bromeliad prey base are exploited by other specialist bird species (see Appendix). Some dendrocolaptids, especially *Nasica longirostris* and scythebills (*Camplylorhamphus* spp.), have long bills, and may be better able to exploit aquatic prey. There are anecdotal accounts of some species, including *P. lawrencii*, taking aquatic vertebrates, such as salamanders and frogs, from bromeliads (e.g., Todd and Carriker 1992; Stiles and Skutch 1989). Only one of 45 bromeliads sampled for this study contained a vertebrate (a small frog), suggesting that vertebrate prey are rare in bromeliads at La Georgina.

Pseudocolaptes lawrencii is a substrate-restricted forager (*sensu* Robinson and Holmes 1982) whose foraging behavior and prey choice are mediated by the nature of its foraging substrate. This species selectively forages in leaf-litter and organic debris trapped in large arboreal bromeliads, which have the greatest diversity and quantity of prey items. When *P. lawrencii* find suitable substrates, they opportunistically consume prey, in terms of both prey size and prey composition, as it is encountered. Rosenberg (1993) documented a similar phenomenon among *Myrmotherula* antwrens specialized on foraging in suspended aerial leaf-litter. Specialist antwrens foraged in curled dead leaves over 90% of the time but took prey roughly in proportion to availability. The existence of highly specialized and stereotyped behaviors that limit foraging to a narrow range of substrates implies that these substrates have been predictable and productive sources of food over evolutionary time (Rosenberg 1993). Arthropods associated with leaf-litter should therefore be predictable and abundant year-round in arboreal bromeliads at La Georgina. In contrast, bromeliad-inhabiting aquatic invertebrates may be highly ephemeral and thus unpredictable from the bird's perspective. However, the seasonality of the bromeliad prey base remains to be quantified.

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APPENDIX

FIFTY-ONE NEOTROPICAL BIRD SPECIES RECORDED FORAGING FOR ANIMAL PREY IN BROMELIADS. SP = PROBABLE FORAGING SPECIALIST; DL = RECORDED FORAGING IN DEAD, CURLED BROMELIAD LEAVES OR INFLORESCENCES, NOT PLANT INTERIOR

Family	Scientific name	Common name	Notes	Reference
Accipitridae	*Geranospiza caerulescens*	Crane Hawk		21, 22
Picidae	*Picoides villosus*	Hairy Woodpecker		17
	Piculus rubiginosus	Golden-olive Woodpecker		1
Furnariidae	*Cranioleuca marcapatae*	Marcapata Spinetail		11
	Margarornis stellatus	Star-chested Treerunner		15
	M. bellulus	Beautiful Treerunner		16
	Anabacerthia striaticollis	Montane Foliage-gleaner		23, 5
	A. variegaticeps	Spectacled Foliage-gleaner		13
	Pseudocolaptes lawrencii	Buffy Tuftedcheek	SP	21, 19, 28, 5, 17
	P. boissonneautii	Streaked Tuftedcheek	SP	5, 3, 15
	P. johnsoni	Pacific Tuftedcheek	SP	15
	Hyloctistes subulatus	Striped Foliage-gleaner		5, 22
	Syndactyla (Automolus) ruficollis	Rufous-necked Foliage-gleaner		12, 15
	Automolus ochrolaemus	Buff-throated Foliage-gleaner		21
	Cichlocolaptes leucophrus	Pale-browed Treehunter	SP	15
	Thripadectes rufobrunneus	Streak-breasted Treehunter		21, 19, 22
Dendrocolaptidae	*Nasica longirostris*	Long-billed Woodcreeper	SP	5, 15
	Xiphocolaptes albicollis	White-throated Woodcreeper	SP	15
	X. falcirostris	Moustached Woodcreeper	SP	15
	X. promeropirhynchus	Strong-billed Woodcreeper	SP	23, 5
	Xiphorhynchus flavigaster	Ivory-billed Woodcreeper	DL	27
	Campylorhamphus trochilirostris	Red-billed Scythebill		26, 4, 15
	C. procurvoides	Curve-billed Scythebill		5, 15
	C. falcularius	Black-billed Scythebill		15
	C. pusillus	Brown-billed Scythebill		5, 22
Corvidae	*Cyanolyca argentigula*	Silvery-throated Jay		22, 18
Troglodytidae	*Campylorhynchus zonatus*	Banded-backed Wren		19, 22
	Troglodytes aedon	House Wren		9
	T. ochraceus	Ochraceous Wren		9
Mimidae	*Cinclocerthia ruficauda*	Trembler	SP	29
Parulidae	*Vermivora gutturalis*	Flame-throated Warbler	DL	17
	Dendroica dominica	Yellow-throated Warbler		8

APPENDIX

CONTINUED

Family	Scientific name	Common name	Notes	Reference
Thraupidae	*Orchesticus abeillei*	Brown Tanager		6
	Orthogonys chloricterus	Olive-green Tanager		6
	Buthraupis arcaei	Blue-and-gold Tanager		6
	Wetmorethraupis sterrhopteron	Orange-throated Tanager		6
	Delothraupis castaneoventris	Chestnut-bellied Mountain-Tanager		6
	Chlorochrysa phoenicotis	Glistening-green Tanager		6
	Tangara chilensis	Paradise Tanager		6
	T. icterocephala	Silver-throated Tanager		6
	T. vassorii	Blue-and-black Tanager		6
	Dacnis hartlaubi	Turquoise Dacnis		6
	D. venusta	Scarlet-thighed Dacnis		9
	D. cayana	Blue Dacnis		6
Cardinalidae	*Caryothraustes poliogaster*	Black-faced Grosbeak		20
Icteridae	*Nesopsar nigerrimus*	Jamaican Blackbird	SP	7, 2, 10
	Oreopsar bolivianus	Bolivian Blackbird		14
	Icterus chrysater	Yellow-backed Oriole		10
	Cacicus uropygialis	Scarlet-rumped Cacique		20, 14
	Psarocolius wagleri	Chestnut-headed Oropendola		24
	P. montezuma	Montezuma Oropendola		25

(1) Askins 1983; (2) Cruz 1978; (3) Fjeldså and Krabbe 1990; (4) Friedmann and Smith 1950; (5) Hilty and Brown 1986; (6) Isler and Isler 1987; (7) Lack 1976; (8) Lack and Lack 1972; (9) Nadkarni and Matelson 1989; (10) Orians 1985; (11) Parker and O'Neill 1980; (12) Parker et al. 1985; (13) Ridgely and Gwynne 1989; (14) Ridgely and Tudor 1989; (15) Ridgely and Tudor 1994; (16) Robbins et al. 1985; (17) Sillett 1994; (18) Sillett, pers. observation; (19) Skutch 1969; (20) Skutch 1972; (21) Slud 1964; (22) Stiles and Skutch 1989; (23) Todd and Carriker 1922; (24) M. S. Webster *in litt.*; (25) M. S. Webster unpubl. ms; (26) Wetmore 1927; (27) Willis 1960; (28) Wolf 1976; (29) Zusi 1969.