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FORAGING ECOLOGY OF EPIPHYTE-SEARCHING INSECTIVOROUS BIRDS IN COSTA RICA[1]

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Abstract. Foraging ecology and diet of eight species of epiphyte-searching insectivorous birds were studied in the Talamanca mountains of Costa Rica to determine degree of epiphyte specialization. To measure species' selectivity for epiphytic substrates, quantitative data on epiphyte availability was compared to actual bird use of epiphytes. Associations between each species and its foraging substrates, foraging maneuvers, and diets suggested a continuum in foraging behaviors across the eight species. At one end of this continuum were substrate-restricted species, whose foraging behavior and prey choice appear to have been mediated by the nature of their foraging substrates. At the other end of the continuum were prey-specific species, whose foraging behavior and substrate choice appear to have been determined by the nature of their prey. Four species in the study area (approximately 8% of the resident avifauna) were epiphyte specialists: *Pseudocolaptes lawrencii* on arboreal bromeliads, *Margarornis rubiginosus* on bryophytes, *Lepidocolaptes affinis* on bryophytes and foliose lichens, and *Troglodytes ochraceus* on epiphytic root masses.

Key words: Epiphytes; foraging ecology; Neotropics.

Resumen. La dieta y aspectos ecológicos del forrajeo fueron estudiados en ocho (8) especies de aves insectívoras que buscan su alimento en plantas epífitas en las montañas de Talamanca, Costa Rica, para determinar el grado de especialización en estas plantas epífitas. Para medir la selectividad de las especies por el substrato epifítico, datos cuantitativos sobre la disponibilidad de las plantas epífitas fueron comparados con el uso que las aves hacen de esas plantas. Asosiaciones entre cada especie de aves, su substrato y las maniobras de forrajeo, con su dieta sugirieron un continuo en el comportamiento alimenticio a traves de las ocho especies estudiadas. En uno de los extremos de dicho continuo estuvieron las especies restringidas-al-substrato cuyo comportamiento alimenticio y la selección de las presas parecieron estar determinadas por la naturaleza de su substrato de forrajeo. En el otro extremo del continuo estuvieron las especies restringidas-a-la-presa cuyo comportamiento alimenticio y selección del substrato parecieron determinados por la naturaleza de sus presas. Cuatro especies en el área (aproximádamente 8% de la avifauna residente) resultaron ser especialistas en las epífitas *Pseudocolaptes lawrencii* en bromelias arboreas, *Margarornis rubiginosus* en briofitas, *Lepidocolaptes affinis* en briofitas y liquenes foliosos y *Troglodytes ochraceus* en masas de raices epífitas.

Palabras clave: Epífitas; ecología de forrajeo; Neotrópico.

INTRODUCTION

One explanation for high bird species diversity in Neotropical forests is foraging specialization on resource types not available in the Temperate Zone (Schoener 1968, Orians 1969, Karr 1971, Terborgh 1980, Remsen 1985). Bird specialization on these "novel" tropical resources, such as abundant suspended aerial leaf-litter (Gradwohl and Greenberg 1982; Remsen and Parker 1984; Rosenberg 1990a, 1990b), army ants (Willis and Oniki 1978), riverine habitats (Remsen and Parker 1983, Rosenberg 1990), and bamboo (Parker 1982; Parker and Remsen, unpubl. data; Kratter, unpubl. data), has been well-documented. In Amazonia, these four resource types account, in part, for approximately 20% of bird species diversity; in the Nearctic region, these resources are rare or lacking altogether.

Another "novel" tropical resource is the abundant and diverse epiphytic vegetation found in cloud forests and other tropical montane forests. Epiphytes increase structural complexity of forests and provide food resources in addition to those borne directly by trees. Canopy soil and detritus, collectively called crown humus, and

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non-vascular epiphytes (bryophytes and lichens) support diverse invertebrate communities (Gerson and Seaward 1977, Gerson 1982, Nadkarni and Longino 1990). Vascular epiphytes, which include bromeliads, orchids, ferns, herbs, and woody shrubs, provide fruit and flowers (Benzing 1987, Gentry and Dodson 1987) and invertebrate prey (Picado 1911, Laessle 1961, Paoletti et al. 1991). Although some forest types along the Pacific coast of North America are draped with luxuriant epiphytic growth, no Nearctic birds are documented as epiphyte specialists. Some species, however (e.g., Brown Creeper, *Certhia familiaris* [Stiles 1978]), may frequently use epiphytes in parts of their range or during parts of the year.

Bird use of epiphytes in the Neotropics is poorly known (see Nadkarni and Matelson [1989] for a literature review). Only two studies have quantified use of epiphytes and epiphyte specialization by Neotropical insectivorous birds (Remsen 1985, Nadkarni and Matelson 1989). However, neither study was designed to quantify availability of epiphytes. An index of epiphyte availability is important because epiphytic vegetation may cover nearly every bark surface in Neotropical montane forests, and use of epiphytes may thus reflect opportunism rather than specialization. I considered a species to be an epiphyte specialist only if it used epiphytes in at least 75% of its foraging attempts (Remsen and Parker 1984) and used at least one epiphyte substrate in a greater proportion than that substrate's availability.

My research focused on the montane avifauna characteristic of eastern Costa Rica and western Panama (Slud 1964; Skutch 1967, 1972; Wetmore 1965, 1968, 1973; Wetmore et al. 1984; Wolf 1976; Ridgely and Gwynne 1989; Stiles et al. 1989). The purpose of this research was to further document the contribution of epiphytes to Neotropical bird species diversity by: (1) determining degree of foraging substrate specialization and resource partitioning among eight species of arboreal, epiphyte-searching insectivorous birds, and (2) measuring the species' selectivity of epiphyte substrates by comparing epiphyte use to quantitative data on epiphyte availability.

STUDY AREA AND METHODS

The study sites were in the Cordillera de Talamanca at approximately 83°40′W, 9°30′N, around kilometer 95 on the Pan American Highway near the Pensión La Georgina in Villa Mills, Costa Rica (hereafter "La Georgina"). All data were collected from 3 July to 11 August 1991, between 2,800 and 3,100 m in elevation. The montane rain forest (sensu Holdridge 1967) around La Georgina is near the transition zone from oak forest to páramo vegetation. *Quercus costaricensis* is the dominant canopy tree; other common tree species are *Miconia bipulifera, Vaccinium consanguineum, Weinmannia pinnata,* and *Didymopanax pittieri* (Holdridge et al. 1971, Hartshorn 1983).

Most trees were covered with epiphytic vegetation; the most conspicuous types were bryophytes, lichens, and large tank bromeliads. The shrub layer was dominated by bamboo (*Chusquea* sp.), all of which, except in ravine bottoms, was dead as a result of a mass-flowering in late 1989 (J. Sanchez, pers. comm.). Much of the oak forest in the Villa Mills area has been degraded by logging and charcoal making (Hartshorn 1983). Relatively undisturbed forest occurs away from the Pan American highway and on steeper slopes.

I selected three trails cut through the forest as my study sites. Two trails were on the Caribbean side of the Continental Divide and had a 30–35 m forest canopy. On the Pacific side, the forest along the third trail was more disturbed from past logging, with canopy height 20–30 m (although some individual trees were taller). The trails were far enough apart that I was confident that the sites did not share the same individual birds. The owner of La Georgina did not allow cutting trees or charcoal making on his property (M. Herrera, pers. comm.); thus, recent logging was not evident at any sites.

I studied eight species of epiphyte-searching insectivores at La Georgina: *Lepidocolaptes affinis* (Spot-crowned Woodcreeper, Dendrocolaptidae), *Margarornis rubiginosus* (Ruddy Treerunner, Furnariidae), *Pseudocolaptes lawrencii* (Buffy Tuftedcheek, Furnariidae), *Troglodytes ochraceus* (Ochraceous Wren, Troglodytidae), *Vireo carmioli* (Yellow-winged Vireo, Vireonidae), *Chlorospingus pileatus* (Sooty-capped Bush-Tanager, Thraupidae), *Vermivora gutturalis* (Flame-throated Warbler, Parulidae), and *Myioborus torquatus* (Collared Redstart, Parulidae). Nomenclature follows AOU (1983). All eight species were primarily arboreal and frequently participated in mixed-species flocks. I did not include primarily frugivorous species, terrestrial

or undergrowth species, which often foraged in dense bamboo thickets, or sallying species, such as *Empidonax atriceps* (Black-capped Flycatcher).

Birds were opportunistically encountered as I slowly walked through the study sites. I worked a given site about once every three days. All observations were taken between 06:00 and 13:00 hr because rain and wind made finding and observing birds difficult later in the day. I tried to take only one observation per individual bird per day to minimize sequential observations and to avoid serial correlation problems during data analysis (Martin and Bateson 1986, Hejl et al. 1990). This procedure maximized the number of independent foraging observations from each site, but limited my total sample size because flocks or solitary individuals were often scarce or fast-moving.

For each foraging individual, I recorded the following data onto microcassette: estimated height above ground and distance to canopy, foliage density (measured on a subjective scale from 1–5 in a 1-m-diameter sphere around the bird), foraging maneuver, substrate type, perch type, and perch size. My classification of behaviors followed Remsen and Robinson (1990). Non-epiphyte substrate categories were: "leaf," "leaf axil," "dead leaf," "bark," "fruit or flower," and "air." Eiphyte substrate categories included: "mat bryophyte" (any appressed growth-form), "pendant bryophyte" (any hanging growth-form), "fruticose lichen" (e.g., species of *Usnea* and *Alectoria*), "foliose lichen" (e.g., species of *Lobaria* and *Parmelia*), "tank bromeliads" (e.g., species of *Guzmania, Vriesea,* and *Tillandsia* [Burt-Utley and Utley 1977]), "root mass" (included the root masses of all vascular epiphytes), and "leaf" (included the leaves of all vascular epiphytes except bromeliads). Vascular epiphytes, other than bromeliads, were relatively rare in the forest, making unnecessary a finer partitioning of the epiphyte leaf and root mass categories (see Nadkarni and Matelson 1989). Few epiphytic angiosperms were in fruit or flower, and none of the bird species that I studied used these resources during my stay at La Georgina. It was often impossible to estimate perch size for birds perched on their foraging substrate; therefore, perch size data did not include substrate perches.

Birds were collected with shotguns in the vicinity of the study sites for analysis of stomach contents. I also collected specimens of *Picoides villosus* (Hairy Woodpecker, Picidae) for a diet comparison with the eight study species. By quantifying the diet of *P. villosus,* which fed primarily by hammering holes in bark and dead wood (pers. observ.), I was able to indirectly compare the prey base found under bark and in dead wood with the prey base in bark-dwelling epiphytes and associated organic debris, as represented by diets of the other eight species. Specimens were prepared as either study skins or skeletons; tissue samples from each bird were preserved in liquid nitrogen. All 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 order under a 6×–50× 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), Borror et al. (1989), and Chapman and Rosenberg (1991). I believe that with knowledge of the particular fragments representing the different types of arthropods, I was 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 and require further experimentation (Rosenberg and Cooper 1990 and references therein).

To quantify availability of foraging substrates, two assistants conducted vegetation surveys along the three trails. At 40 randomly selected points along each trail, imaginary 1-m-diameter cylinders were delineated, extending from ground to the forest canopy. For every branch or other woody tissue that intersected a cylinder, height and presence or absence of eight substrate classes: seven epiphyte categories (described above) and one general non-epiphyte category (included all non-epiphyte categories above except air) were recorded.

DATA ANALYSIS

The categorical variables "foraging maneuver" and "foraging substrate" were statistically compared among species with contingency tables, using Statview II (Abacus Concepts 1991). The null

hypotheses for these contingency tables were that the species did not differ in their use of foraging substrates and foraging maneuvers. I then analyzed the table cell residuals, or the discrepancies between the observed and expected values for each cell (Siegel and Castellan 1988). Analysis of residuals identifies the cells of a contingency table responsible for an overall, significant G-statistic. This residual analysis identified the species whose use of specific substrates or maneuvers significantly differed from the expected behavior of a strictly generalist forager. Use of foraging maneuver and foraging substrate did not differ among the three sites for any of the species (Sillett 1992). Given that substrate availability also did not differ among sites (see below), I pooled foraging observations from the three sites for all species comparisons.

Conservatively, no more than 20% of the cells in a contingency table should have an expected frequency of less than five, and no cell should have an expected frequency of less than 1 (Cochran 1954). Therefore, I combined some substrate and foraging maneuver categories. Revised substrate categories were: "leaf" (all non-epiphyte foliage), "other non-epiphyte" (fruit, bark, air), "bryophyte mat," "pendant epiphyte" (fruticose lichen and pendant bryophyte), "bromeliad," and "other epiphyte" (root mass, foliose lichen, and epiphyte leaf). Revised foraging maneuver categories were: "glean," "probe" (included prying with the bill), "pull," "hang," "reach," and "acrobatic" (all sallies, lunges, leaps, and flush-pursuits). See Remsen and Robinson (1990) for a complete description of the foraging maneuver categories.

To test if species significantly differed in diet, I used discriminant analysis (DISCRIM procedure of SAS/STAT, SAS Institute 1992), where each individual stomach sample was considered as an independent replicate. Because variance-covariance matrices for all species were not equal, I used nonparametric, or kernel discriminant analysis (Titterington 1980, Hand 1983). To control experiment-wide error rate, I considered species to be significantly different in diet if the probability of a greater Mahalanobis distance was less than $P = 0.01$ for pairwise comparisons. I created nine prey categories, based on prey behavior (sensu Cooper et al. 1990), to simplify analyzing and discussing diets. The categories were: "Coleoptera," "Orthoptera" (included roaches), "Dermaptera," "Heteroptera" (Hemiptera and Homoptera), "egg case" (roach egg cases—many stomachs had egg cases without any evidence of having eaten roaches), "active fliers" (Diptera and Hymenoptera), "cryptic fliers" (nocturnal or weak-flying insects, e.g., Lepidoptera: moths, Psocoptera, and Neuroptera), "arachnid" (spiders, pseudoscorpions, and harvestmen), and "larvae" (all insect larvae, plus rarely encountered isopods and millipedes).

I did not directly measure arthropod variability on different substrates. However, variation in resource use among individual birds may provide an indirect measure of resource predictability from the bird's perspective (Sherry 1984, 1990). To determine if there were any relationships between resource predictability and stereotypy in foraging behavior, I calculated population dietary heterogeneity (PDH, Sherry 1984), an index of the extent of variability in arthropod resource use for each bird species. PDH = G/(df), where G = the G-statistic (Sokal and Rohlf 1981) for the comparison of diet among conspecifics, and df = degrees of freedom for each comparison. Species with a relatively high PDH have a high degree of inter-individual variation in diet.

Availability of the eight substrate categories was calculated as follows. I combined the data from all study sites to yield an overall estimate of substrate availability at La Georgina, because only one of the seven substrate categories, pendant bryophytes, differed in availability among the three sites (analysis of variance, $F_{2,117} = 4.229$, $P = 0.0169$). Within each of the 120 cylinders, I determined percentage of branches (or other woody tissues) having each of the eight substrate categories. For example, a cylinder crossed by four branches, two of which had pendant bryophytes, had a pendant bryophyte "score" of 0.50. The substrate "scores" were then summed for all cylinders and divided by 120 to give a mean availability measure for each substrate. This mean equaled the chance of a randomly selected branch having a particular substrate. Many branches supported multiple types of epiphytes, so the sum of the means was greater than 1.0. Therefore, I converted means to relative proportions by summing all substrate means and then dividing each substrate mean by this total. These proportions equaled the chance a foraging bird encountered a substrate if it landed at a random point on a random branch. These relative substrate pro-

TABLE 1. Body mass and foraging site characteristics of eight epiphyte-searching bird species in Costa Rica. Species differences in foraging height and foraging perch size were examined with analysis of variance, blocking on study site. All terms in the analyses were fixed. The species differed in perch size ($F_{6, 12} = 16.61$, $P < 0.0001$) but not in foraging height ($F_{7, 14} = 1.96$, $P = 0.134$). *Pseudocolaptes lawrencii* was not included in the perch size comparison because of the small sample for perch size for this species, which primarily perched on its foraging substrate.

Species	Code	Body mass[a]	% Foliage column[b] mean ± SE (*n*)	Perch diameter (cm)[c] mean ± SE (*n*)	Foliage density[d] mean ± SE (*n*)
Lepidocolaptes affinis	LA	35.4	0.59 ± 0.04 (53)	24.9 ± 2.9 (53)[1]	1.8 ± 0.13 (53)
Margarornis rubiginosus	MR	18.0	0.53 ± 0.02 (132)	14.7 ± 1.4 (116)[2,3]	2.8 ± 0.07 (132)
Pseudocolaptes lawrencii	PL	50.9	0.66 ± 0.02 (78)	9.5 ± 1.6 (23)	2.9 ± 0.09 (75)
Troglodytes ochraceus	TO	10.5	0.57 ± 0.03 (51)	17.2 ± 2.7 (47)[2]	3.5 ± 0.13 (51)
Vireo carmioli	VC	14.1	0.60 ± 0.03 (38)	1.7 ± 0.4 (35)[4]	3.7 ± 0.15 (38)
Chlorospingus pileatus	CP	20.7	0.51 ± 0.03 (99)	2.7 ± 1.0 (97)[4]	4.0 ± 0.09 (99)
Vermivora gutturalis	VG	11.0	0.66 ± 0.03 (82)	1.4 ± 0.3 (78)[4]	4.2 ± 0.10 (82)
Myioborus torquatus	MT	10.7	0.47 ± 0.04 (54)	10.7 ± 2.0 (52)[3]	3.1 ± 0.15 (54)

[a] Mean of 10 specimens (7 for *T. ochraceus*) collected for this study (in grams).
[b] Represents foraging height standardized among sites; % Foliage column = foraging height/canopy height.
[c] Species that do not share the same superscript number were significantly different ($\alpha \leq 0.05$) from each other in mean perch size based on Duncan's multiple range test (Duncan 1955).
[d] Measured on a scale from 1–5; see Methods.

portions were directly comparable to the bird species' proportional use of the same substrate categories.

To measure bird species selectivity for the substrate categories, I subtracted the proportional species use of each foraging substrate from each substrate's proportional availability. I then calculated 95% confidence intervals (CI) for the relative proportional availability of the eight substrate categories. I considered a species to use a substrate selectively (significantly more than expected by chance) if use minus availability was positive and >CI for the substrate. Conversely, I considered a species as significantly avoiding a substrate if use minus availability was negative and <CI.

RESULTS

FORAGING DATA

The eight species differed in body size and foraging site characteristics (Table 1), and used a range of foraging substrates (Figs. 1a, b) and foraging maneuvers (Fig. 2). *Lepidocolaptes affinis* foraged in typical dendrocolaptid fashion, climbing up trunks and larger branches and probing its bill into and under substrates. *L. affinis* also used its decurved bill to pry, or lift substrates up away from bark, presumably to capture hidden arthropods; it was the only species to feed extensively under foliose lichens (Fig. 1b). *L. affinis* was a silent and inconspicuous forager. *Margarornis rubiginosus* (hereafter *M. rubiginosus*), also climbed up trunks and branches; however, it used smaller perches (Table 1) than *L. affinis*. *M. rubiginosus* frequently foraged on undersides of branches, and clung to pendant bryophytes as it probed into them. *M. rubiginosus* was an active, easily observable member of mixed-species flocks. *Pseudocolaptes lawrencii* (hereafter *P. lawrencii*) was the most substrate-specific forager: 74% of foraging observations were on bromeliads (Fig. 1b). *P. lawrencii* was often noisy and conspicuous as it foraged in bromeliads, vigorously pulling out and tossing aside trapped leaf litter and other debris. *P. lawrencii* joined mixed-species flocks, but usually lagged behind faster-foraging species. *Troglodytes ochraceus* was primarily a probing species, sometimes hanging or reaching to get under and inside substrates (Fig. 2); it was the only species to extensively forage in the humus around epiphyte root masses (37% of observations; Fig. 1b). This species also uses epiphyte root masses in Monteverde, Costa Rica (Nadkarni and Matelson 1989). *T. ochraceus* was an active, almost fossorial forager, often disappearing from view as it clambered inside root masses or under partially detached bryophyte mats; its foraging habits sometimes prevented detailed observation. *Vireo carmioli* (hereafter *V. carmioli*) frequently leaped or lunged at substrates to capture prey (Fig. 2); it was unclear whether or not these leaps were actually short sallies, however. *V. carmioli* often appeared to

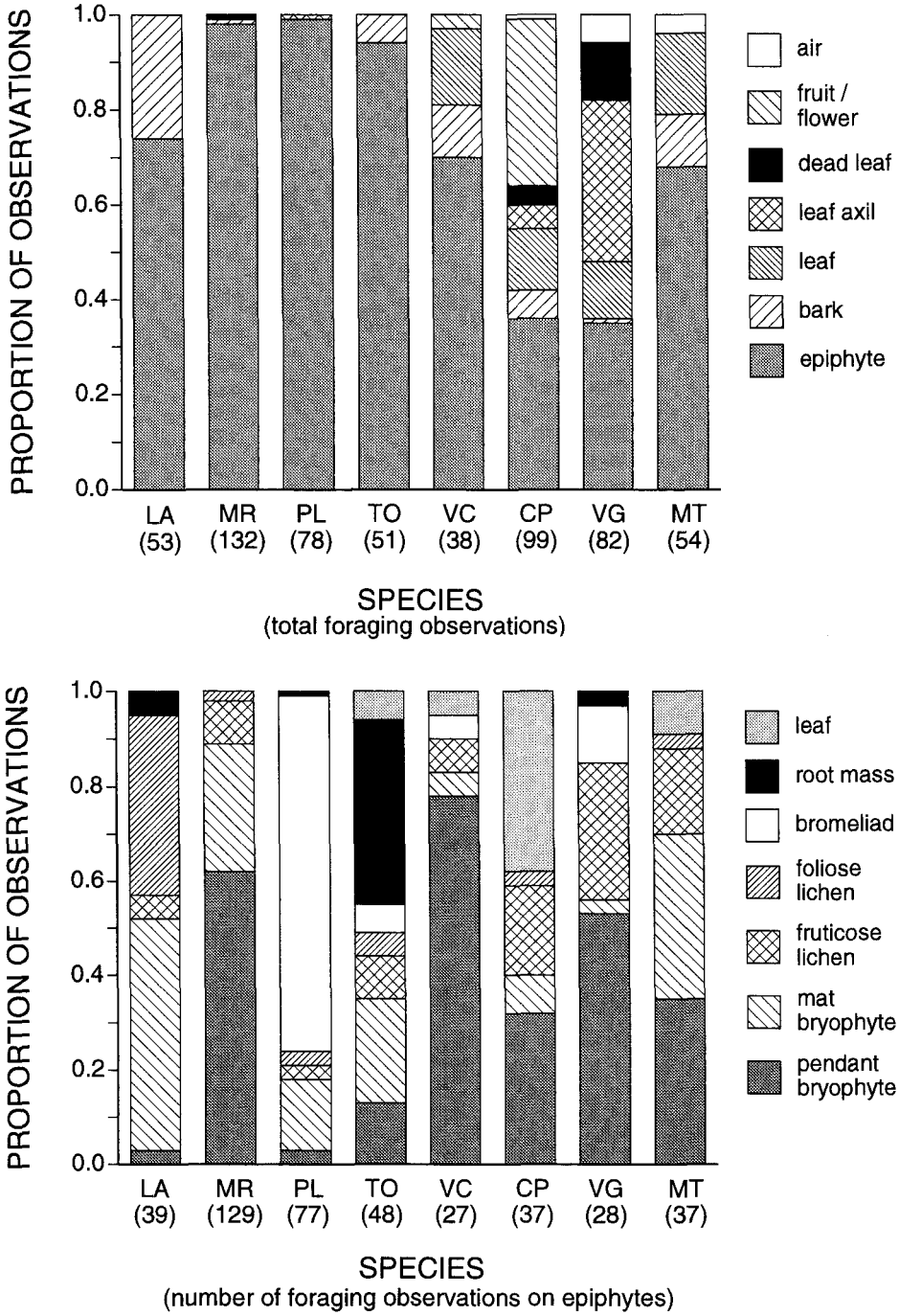

FIGURE 1. Top: General use of different substrates by eight species of epiphyte-searching insectivores in Costa Rica; species codes given in Table 1. See Methods for description of substrate categories. Bottom: Epiphyte substrate use by eight species of epiphyte-searching insectivores in Costa Rica.

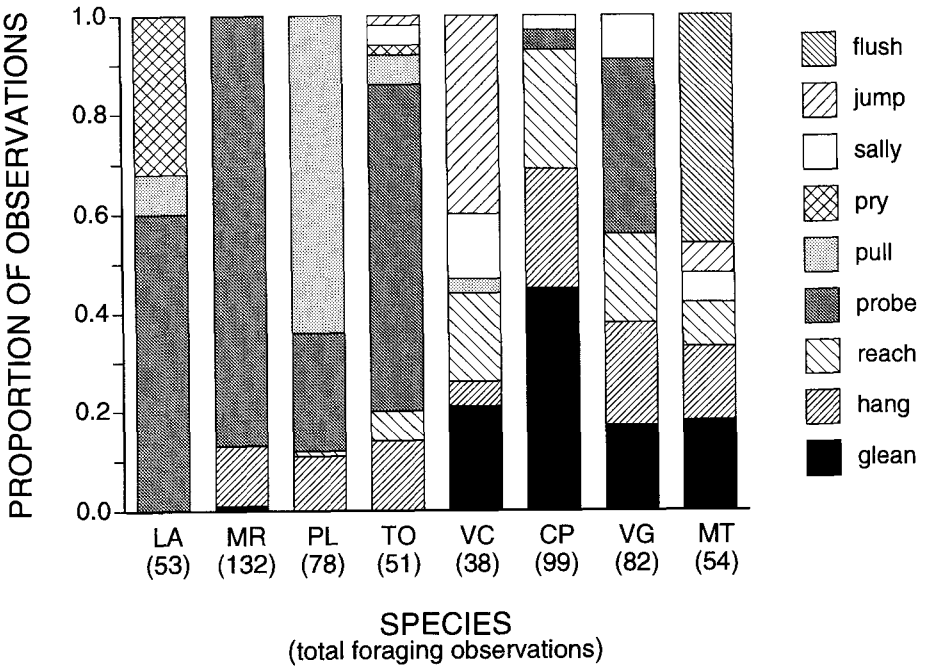

FIGURE 2. Foraging maneuvers used by eight species of epiphyte-searching insectivores in Costa Rica; species codes given in Table 1. See Methods for description of substrate categories.

leap or lunge after flushed arthropods. Because of its cryptic coloration and darting method of foraging, *V. carmioli* was the most difficult species to observe. *Chlorospingus pileatus* used the widest range of substrates and was the only species to consistently feed on fruit (Fig. 1a). Hanging and reaching accounted for 48% of observed *C. pileatus* foraging maneuvers. *C. pileatus* was the most vocal, conspicuous member of the guild, and most mixed-species flocks seemed to organize around this species. *Vermivora gutturalis* (hereafter *V. gutturalis*) frequently used the hang and reach maneuvers while probing with its bill into live foliage. However, it may have actually been gaping (probing its bill into substrates and then opening the bill to widen the opening) when foraging on curled dead leaves, dead bromeliad inflorescences, or clusters of leaf axils. Gaping is used by other species of Vermivora (Ficken and Ficken 1968). *Myioborus torquatus* (hereafter *M. torquatus*), like other *Myioborus* (Ridgely and Tudor 1989), habitually fanned its tail to flash the white outer rectrices while foraging. Forty-six percent of observations were flushes (Fig. 2), where the bird presumably flushed a hiding arthropod with its spread tail.

The eight species were significantly different in their use of foraging maneuvers ($G_{35} = 770.29$, $P < 0.0001$) and foraging substrates ($G_{35} = 706.08$, $P < 0.0001$). *P. lawrencii* was the most differentiated species, due to its stereotypic foraging mode: pulling trapped leaf-litter out of bromeliads with its bill in search of arthropods (analysis of contingency table residuals, Appendix 1). Probing with the bill and foraging in foliose lichens or pendant epiphytes most clearly separated *L. affinis* from the other species (Appendix 1). *M. rubiginosus* was strongly associated with probing and foraging in pendant epiphytes. Foraging in root masses of epiphytic angiosperms distinguished *T. ochraceus* (Appendix 1). *C. pileatus* primarily differed from the other species because it gleaned fruit. *V. gutturalis* was most associated with foraging in live foliage, while *V. carmioli* and *M. torquatus* were strongly associated with "acrobatic" foraging maneuvers (Appendix 1).

DIETS

Only animal matter is included in the diet information presented below for the eight species of epiphyte-searching insectivores, plus the

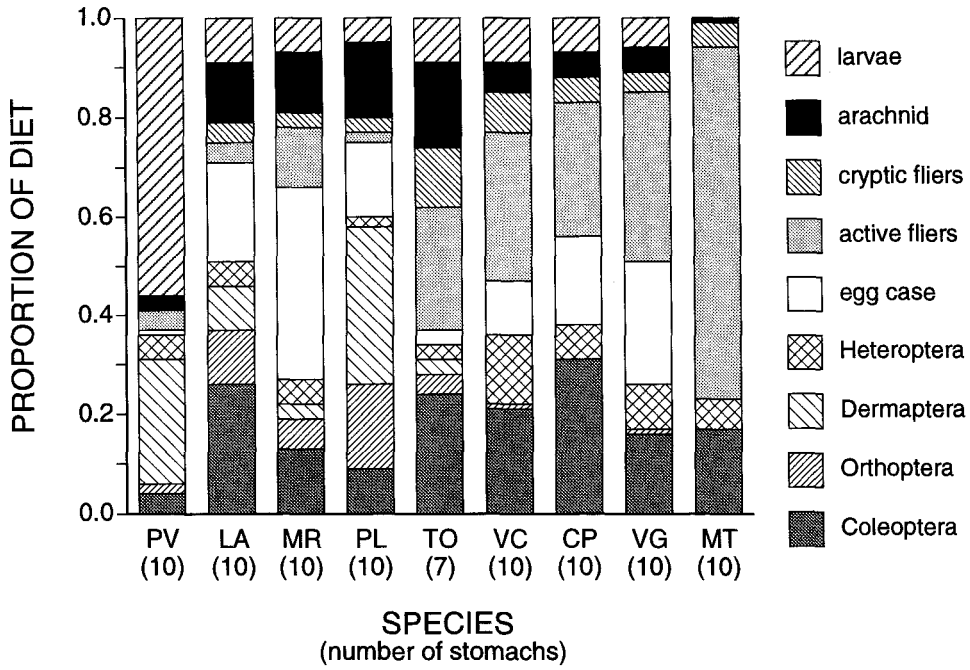

FIGURE 3. Diets of nine species of insectivores in Costa Rica. Diet was determined for each species by averaging the proportions of prey categories across individuals. PV = *Picoides villosus*; other species codes given in Table 1. See Methods for description of prey categories.

woodpecker, *Picoides villosus*. The only species to frequently consume fruit was *C. pileatus*, and all stomachs examined from this species usually contained several dozen fruit seeds. It was impossible to relate number of seeds in a stomach to number or volume of fruits eaten because some fruits examined at La Georgina contained many seeds (pers. observ.).

All nine species ate a wide variety of arthropod prey (Fig. 3). The most common prey types were Coleoptera, roach egg cases, and "active flier" insects. The diets of two species were dominated by single prey categories: 56% of the diet of *Picoides villosus* (hereafter *P. villosus*) was insect (mostly Coleoptera) larvae, whereas 71% of the diet of *M. torquatus* was "active flier" insects. *P. villosus* and *P. lawrencii* were the only species to consume large amounts of Dermaptera (25% and 32% of the diet, respectively). *M. rubiginosus* was distinguished from the other species by the high proportion of roach egg cases in its diet (Fig. 3). *T. ochraceus, V. carmioli, C. pileatus, V. gutturalis,* and *M. torquatus* ate many more winged prey than did *P. villosus, L. affinis, M. rubiginosus,* and *P. lawrencii*. Besides the exceptions noted below, all species were significantly different from each other in diet (discriminant analysis, $F_{9,70} > 2.82$, $P < 0.0068$). Three species, *V. carmioli, C. pileatus,* and *V. gutturalis,* were not significantly different from each other in diet (discriminant analysis, $F_{9,70} < 2.54$, $P > 0.01$). *Troglodytes ochraceus* was not different from *V. carmioli* and *C. pileatus* (discriminant analysis, $F_{9,70} < 2.54$, $P > 0.01$), but did differ from all other species.

TABLE 2. Population dietary heterogeneity (PDH) values for nine Costa Rican bird species.

Species	PDH
Chlorospingus pileatus	4.34
Vireo carmioli	3.58
Picoides villosus	3.48
Pseudocolaptes lawrencii	2.96
Margarornis rubiginosus	2.57
Vermivora gutturalis	2.53
Lepidocolaptes affinis	2.45
Myioborus torquatus	1.94
Troglodytes ochraceus	1.69

Population diet heterogeneity (PDH) also dif-

fered among the species (Table 2). *Chlorospingus pileatus,* which used the widest range of substrates (Figs. 1a, b), had the highest PDH value, indicating high inter-individual variation in diet. *Pseudocolaptes lawrencii* and *M. rubiginosus,* however, which were the most substrate-specific foragers (Figs. 1a, b), did not have the lowest PDH values. *Troglodytes ochraceus* had the most homogeneous diet, followed by *M. torquatus.*

SUBSTRATE USE VERSUS AVAILABILITY

The eight species widely differed in their selectivity for foraging substrates (Fig. 4). All cases of substrate selectivity or avoidance presented below are statistically significant at the $\alpha = 0.05$ level. Non-epiphyte substrates occurred on nearly every vegetation intersection in the cylinders (Table 3). Pendant bryophytes were the most common epiphytic substrate. Vascular epiphyte leaves were the rarest substrate. Three species, *M. rubiginosus, P. lawrencii,* and *T. ochraceus,* avoided non-epiphytic substrates (Fig. 4). *P. lawrencii* was highly selective of bromeliads, *M. rubiginosus* selected bryophytes, and *T. ochraceus* selected epiphyte root masses and, to a lesser degree, mat bryophytes. *L. affinis, V. carmioli,* and *M. torquatus* used non-epiphytic substrates in proportion to availability. *L. affinis* selected foliose lichens and mat bryophytes, and *V. carmioli* and *M. torquatus* selected bryophyte substrates. *C. pileatus* and *V. gutturalis* selected non-epiphytic substrates and avoided epiphytes (Fig. 4). All species tended to avoid fruticose lichens ($G_7 = 139.10$, $P < 0.0001$).

TABLE 3. Availability of eight substrate categories at La Georgina. Mean substrate availability was the chance of a randomly selected branch having a particular substrate. The sum of the means was greater than 1.0 because many branches supported multiple types of epiphytes. Relative proportions were generated by summing all substrate means and then dividing each substrate mean by this total. These relative proportions equaled the chance a foraging bird encountered a substrate if it landed at a random point on a random branch.

Substrate	Mean ± S.E.	Relative proportion
Non-epiphyte	0.96 ± 0.02	0.32
Pendant bryophyte	0.64 ± 0.03	0.22
Fruticose lichen	0.54 ± 0.03	0.18
Mat bryophyte	0.24 ± 0.02	0.08
Root cluster	0.20 ± 0.02	0.07
Bromeliad	0.17 ± 0.02	0.06
Foliose lichen	0.15 ± 0.02	0.05
Epiphyte leaf	0.07 ± 0.01	0.02

DISCUSSION

The assemblage of epiphyte-searching insectivores at La Georgina exhibited a continuum of foraging behaviors similar to that observed by Robinson and Holmes (1982) for insectivorous birds in a temperate hardwood forest. One end of this continuum at La Georgina was "substrate-restricted" foraging (Robinson and Holmes 1982). Substrate-restricted foragers specialized on particular substrates, and frequently used their bills or feet to actively manipulate these substrates. An example of substrate-restricted foraging behavior was *P. lawrencii*'s use of the "pull" maneuver on bromeliads. The next class of foraging behavior was "near-surface" foraging (Robinson and Holmes 1982), where species tended to use a range of foraging substrates and captured prey with little substrate manipulation (e.g., *C. pileatus, V. gutturalis*). The other end of the foraging behavior continuum at La Georgina was prey-specific foraging, where species did not manipulate substrates with their bills or feet in search of subsurface prey. Instead, they used quick, darting foraging movements, frequently flushing and pursuing arthropod prey from substrate surfaces (e.g, *M. torquatus,* and possibly *V. carmioli*). The restricted number of foraging maneuvers used by the eight species suggests that their foraging behavior may have been constrained by habitat and prey characteristics (Robinson and Holmes 1982). For example, the frequent use of the "probe" foraging maneuver by *L. affinis, M. rubiginosus,* and *T. ochraceus* suggests that there may be a limited number of ways a bird can search for and capture prey in epiphytic bryophytes and lichens.

Several interesting patterns emerged based on the species' use of foraging behaviors, foraging substrates, and arthropod prey. *M. torquatus, V. gutturalis, C. pileatus, V. carmioli,* and *T. ochraceus,* which usually did not use their bills or feet to manipulate substrates, consumed many more Diptera and Hymenoptera than the other four species. This suggests that these types of prey were easily flushed from substrates and could only be consistently captured by fast, agile bird species. Insect larvae were only frequently eaten by the woodpecker, *P. villosus.* Therefore, larvae were probably most abundant at La Georgina in dead wood and under bark, not on foliage, from

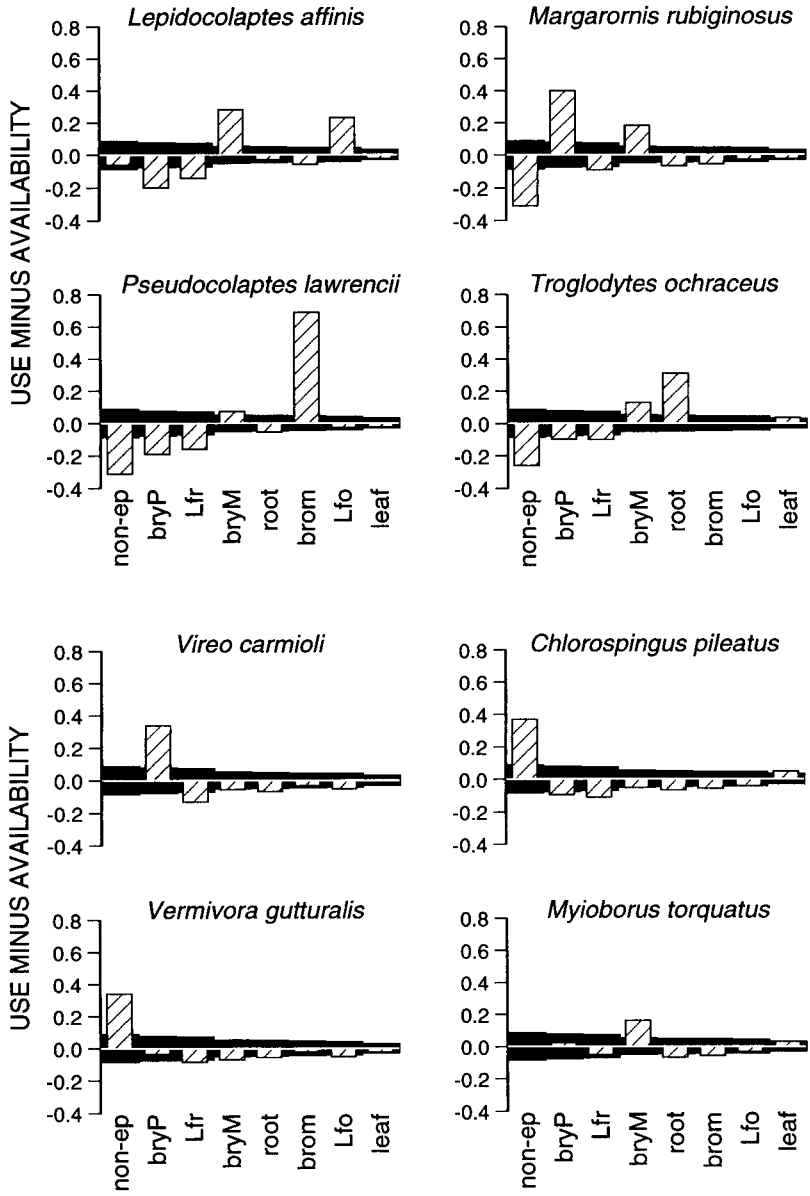

FIGURE 4. Bird use of foraging substrates compared with substrate availability. Scored bars represent use minus availability; black regions represent 95% confidence intervals around substrate availability. Bars falling within the 95% confidence intervals indicate use = availability; bars above the 95% confidence interval indicate significant substrate selection; bars below indicate significant avoidance. Non-ep = all non-epiphyte substrates, bryP = pendant bryophytes, Lfr = fruticose lichen, bryM = mat bryophyte, root = epiphyte root mass, brom = bromeliad, Lfo = foliose lichen, leaf = vascular epiphyte leaf.

June to August 1991. *M. rubiginosus* usually foraged in pendant bryophytes, and consumed many more roach egg cases than the other species. Roach egg cases were not a large proportion of the diet of *V. carmioli*, although it also foraged extensively in pendant bryophytes, indicating that *V. carmioli* may have been keyed into prey with active predator-avoidance responses. *L. affinis*, *M. rubiginosus*, *P. lawrencii*, and *T. ochraceus* frequently foraged in substrates associated with

crown humus, such as mat bryophytes, epiphyte root masses, and bromeliads. These four species in turn ate more arachnids than the other species, suggesting that species that foraged frequently in crown humus may have been more likely to notice cryptic prey. No species was similar to *P. villosus* in diet (Fig. 3), apparently because the prey (e.g., insect larvae) found under bark and in dead wood were different from the prey in bark-dwelling epiphytes and associated organic debris. Similarly, *P. lawrencii* was very distinct from the other species in diet, indicating that bromeliads probably provided a prey resource (e.g., roaches and other orthopterans) different from other substrates. *P. lawrencii* and *P. villosus* were the only species to feed frequently on Dermaptera. These insects may have been relatively abundant in both dead wood and in bromeliads; however, I observed *P. villosus* hammering its bill into the bases of large bromeliads on several occasions. Overall, the relationships among species, substrate, maneuver, and diet suggest a continuum from substrate-intensive foragers, i.e., *P. lawrencii* and *M. rubiginosus,* whose foraging behavior and prey choice may have been mediated by the nature of their foraging substrates, to prey-specific foragers, such as *M. torquatus* and *V. carmioli,* whose foraging behavior and substrate choice may have been determined by the nature of their prey.

Resource predictability seems to favor evolution of foraging specialization (Glasser 1982; Sherry 1984, 1990; Rosenberg 1990a). If true, quantifying the variability in resource types used by conspecifics provides an indirect measure of resource predictability from the species' perspective (Sherry 1984, 1990). Using the Spearman rank correlation (Sokal and Rohlf 1981), I found no correlation between population dietary heterogeneity (PDH) and Brillouin dietary diversity (Hurturbia 1973, Sherry 1984; $r_s = -0.253, P = 0.503$), standardized substrate niche breadth (Hurlbert 1978; $r_s = -0.381, P = 0.313$), or standardized foraging-maneuver niche breadth ($r_s = 0.024, P = 0.950$). Thus, species that were the most stereotyped in use of substrates or foraging maneuvers did not tend to have the most homogeneous diets, or lowest PDH. Likewise, species with the most diverse diets also did not have the highest PDH. Given the substrate-specificity exhibited by *P. lawrencii* and *M. rubiginosus,* and, to a lesser extent, *L. affinis, T. ochraceus,* and *V. carmioli,* this lack of correlations implies that arthropod prey in general was relatively predictable and abundant in bromeliads, bryophytes, and associated crown humus at La Georgina. However, individual prey taxa were probably unevenly distributed on these substrates. Therefore, a relatively high PDH may not necessarily imply ecological opportunism for a species, as suggested by Sherry (1990). Rather, it could indicate that an ecologist's classification of resources (e.g., insect taxa or "ecological" categories) may be different from a bird's definition (e.g., insects = food).

In contrast to my results, Sherry (1984) found a positive correlation between PDH and dietary diversity for 16 species of sallying, insectivorous tyrannids in Costa Rican lowland rainforests; species with the lowest PDH tended to have the most specialized diets. He sampled the diets of these 16 species over a relatively broad geographic range during a three-year period. Lack of PDH-foraging behavior correlations for the nine species at La Georgina may be an artifact of the short duration of my study at a single locality, of my classification of arthropod prey, or of both of these factors. Conversely, Sherry's positive correlations may be because the 16 species he studied tended to be prey-specific, rather than substrate-restricted foragers.

All species tended to avoid fruticose lichens. Certain lichen compounds may have an antiherbivore function and protect the slow-growing thalli from predation (Rundel 1978, Lawrey 1983). In addition, the broad, appressed lobes of foliose lichens probably provide better hiding places for arthropods than the dense, pendant strands of fruticose lichens. These factors could reduce the number of arthropods dwelling in fruticose lichens and may explain the birds' avoidance of this substrate (Fig. 4).

Birds also feed upon epiphytic fruit and flowers, and use epiphytes for nesting material or as nest sites (Nadkarni and Matelson 1989 and references therein). The extent to which bird use of epiphytes varies with season or year remains to be quantified. For example, although the phenology of Neotropical trees has been documented for some localities (e.g., Frankie et al. 1974), almost nothing is known about the phenology of epiphytic angiosperms. Epiphytes may provide critical food to birds when trees are not in fruit or flower. In addition, little is known about the seasonality of epiphyte-inhabiting arthropods.

This study further documents the contribution

of epiphytes to Neotropical bird species diversity and emphasizes the importance of distinguishing among different types of epiphytes used by animals. Epiphytes were an important resource for the birds studied: all eight species used epiphytes in at least 30% of their foraging efforts, and almost all bird species at La Georgina foraged in epiphytes to some extent (pers. obs.). At La Georgina, eight species of insectivores used seven classes of epiphytes. Four insectivorous species, or 8% of the resident avifauna, were epiphyte specialists: *L. affinis, M. rubiginosus, P. lawrencii,* and *T. ochraceus.* These species used epiphytes in at least 75% of their foraging efforts and were selective of particular epiphytic substrates. The specialists all primarily foraged in the various components of the arboreal soil, or crown humus: pendant and mat bryophytes, lichens, root masses, and bromeliads. However, each species differed in its selection of epiphyte resources. *M. rubiginosus* and *P. lawrencii* were highly specialized on particular substrates, selecting bryophytes and bromeliads, respectively.

Finally, montane forests in the Neotropics are being rapidly degraded by logging, grazing, and agriculture (La Bastille and Pool 1978, Zadroga 1981, Stadtmüller 1987). Epiphyte communities may change as forests are degraded, resulting in the loss of sensitive species and an overall decrease in epiphyte species diversity (Hyvönen et al. 1987, Norris 1990, Sillett 1991). Therefore, knowledge of how birds use epiphytes could help predict which bird species would be sensitive to anthropogenic disturbances of montane forest ecosystems.

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APPENDIX 1. Adjusted cell residual values for two contingency tables which compare foraging maneuver and foraging substrate among eight bird species (see Methods). The adjusted residuals have approximately a normal distribution with mean of 0 and standard deviation of 1, and are not independent. Because both contingency tables had >20 cells, I considered cells statistically different from their expected values if $\alpha \leq 0.01$; * = $P \leq 0.01$; † = $P \leq 0.0001$.

Variable	Species (see Table 1 for codes)							
	LA	MR	PL	TO	VC	CP	VG	MT
Maneuver								
glean	−2.97*	−4.78†	−3.69*	−2.9*	1.5	10.13†	1.14	1.23
hang	−3.08*	−0.7	−1.02	−0.05	−1.6	3.23*	1.9	0.19
reach	−2.45*	−4.2†	−2.63*	−0.89	1.98	5.57†	2.99*	−0.03
probe	7.67†	11.7†	−3.53*	3.91†	−5.51†	−8.54†	−1.46	−6.67†
pull	−0.6	−4.32†	17.23†	−1.0	−1.55	−3.61*	−3.23*	−2.55*
acrobatic	−2.67*	−4.56†	−3.32*	−1.2	8.53†	−2.76*	−0.74	11.51†
Sub[1]								
leaf	−3.23*	−5.24†	−3.67*	−3.16*	0.11	2.76*	11.81†	0.32
non-ep.	1.69*	−5.01†	−3.85*	−1.77	0.3	9.81†	−1.91	0.15
bryM	4.13†	3.47*	−0.16	1.13	−2.33	−3.86*	−3.94†	1.69
pendant	−4.47†	10.32†	−5.66†	−2.16	3.7*	−3.25*	−1.07	0.63
bromeliad	−2.69*	−4.6†	19.13†	−1.24	−1.71	−3.85*	−2.31	−2.72*
other ep.	5.42†	−3.47*	−2.03	8.98†	−1.62	−0.83	−2.93*	−0.75

[1] SUB = substrate; non-ep. = other non-epiphyte; bryM = mat bryophyte; other ep. = other epiphyte; see Methods for category descriptions.