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BIRD USE OF EPIPHYTE RESOURCES IN NEOTROPICAL TREES[1]

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Abstract. Epiphytes are a common component of neotropical forests, but their importance to birds at the community level and their role in contributing to tropical bird diversity has only rarely been considered. Literature accounts from 55 studies document 193 species of neotropical birds that take nectar, fruits, invertebrates, water, and nesting materials from epiphytes. To quantify the amounts and types of resources provided by epiphytes compared to host trees, we watched birds in 14 forest and pasture sites (1,350–1,420 m) for 2 months in a lower montane landscape of Costa Rica. During our 289 hr of observations from within the canopy and on the ground, 33 of 56 bird species observed in foraging visits foraged in resources provided by epiphytes. Epiphyte resources were involved in 32% of all foraging visits. For eight bird species, 40% or more of all foraging visits involved epiphyte use, which included foraging for fruits, nectar, invertebrates, water, and nesting materials. Six types of bird foraging behaviors in six types of epiphytes are described and compared to bird use of tree resources. Some birds appeared to specialize on particular epiphyte resources such as invertebrates in crown humus. The frequent epiphyte use by a large number of bird species indicates that epiphytes constitute a resource that has generally been overlooked in past bird community studies. We discuss two ways that epiphytes may contribute to high tropical bird species diversity.

Key words: Epiphytes; canopy; cloud forest; tropical forest; foraging ecology; resource; Monteverde; Costa Rica; community ecology.

INTRODUCTION

Studies of relationships between tropical forest birds and plants have focused almost exclusively on resources provided by trees and understory shrubs. Epiphytes, plants that derive support but not nutrients from their host trees, are a conspicuous component of many tropical and wet temperate forests. They occupy the same physical location as their host trees and produce a diverse array of fruits, nectar, and foliage (Benzing 1987, Gentry and Dodson 1987). Epiphyte biomass varies greatly among forest types; it is largest in neotropical cloud forests, where the live and dead standing crop can exceed 4,800 kg/ha, equivalent to 40% of the total tree, shrub, and understory foliar biomass (Nadkarni 1984). Many tank and rosette epiphytes impound and store water, leaf litter, and dissolved and particulate minerals, which support populations of invertebrates and vertebrates (Picado 1911, Laessle 1961). The dead organic matter that accumulates beneath mats of live epiphytic cryptogams (mosses and liverworts) creates a microhabitat which supports canopy humus invertebrates, including earthworms, millipedes, beetles, and other arthropods (Lyford 1969, Nadkarni and Longino 1988).

Given the great diversity and large biomass of epiphytes in tropical and temperate wet forests (Nadkarni 1984, 1985; Gentry and Dodson 1987), there is surprisingly little data on their use by the animal community. Only a few field studies have mentioned (Orians 1969) or quantified (Remsen 1985) the importance of epiphytes, (primarily mosses) as a resource for tropical birds. Only one study has directly compared temperate vs. tropical epiphyte use by birds (Thiollay 1988). A number of studies focusing on the use of canopy-held dead-leaf litter pointed out the need to distinguish within-canopy resources (Remsen and Parker 1984). However, nearly all the information is scattered in general descriptions of bird behavior and resource use. The technical difficulties of observing birds within the canopy itself have been overcome in only very few studies by using towers, walkways, and mountain-climbing equipment (e.g., Perry 1978, Greenberg 1981, Loiselle 1987). Although a large body of literature on epiphyte taxonomy, physiology, and mineral nutrition exists (Watson et al. 1987), ecological interactions of birds and canopy-dwelling plants have been almost entirely over-

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looked in the literature, except for a few groups such as the hummingbirds (e.g., Feinsinger et al. 1987) and several frugivorous species that disperse mistletoes (e.g., Davidar 1983, Fitzpatrick 1980, Parker 1981, Remsen et al. 1982).

This study is a first step in assessing the overall importance of epiphytes to birds in the tropics. We summarize scattered literature accounts of epiphyte use by birds with respect to bird species, resource types, and epiphyte groups involved. We then present results of a field study that focused on bird and epiphyte interactions in trees of primary forests and pastures in Monteverde, Costa Rica, to ask the following questions: (1) What species of birds are associated with epiphyte use? (2) What is the frequency of bird visits and foraging behavior associated with resources created by epiphytes compared to those of host trees? (3) Which epiphyte groups and epiphyte resources are used by the bird community? (4) Do any birds appear to specialize on particular resources provided by epiphytes or on particular epiphyte groups? (5) What are community-level implications of bird exploitation of epiphyte resources?

LITERATURE REVIEW OF EPIPHYTE USE BY BIRDS

We searched the literature for any references concerning neotropical bird use of epiphytes (except for field identification guides, which almost exclusively describe foraging behaviors anecdotally). We reviewed 55 papers that fell into four categories: (1) frugivory in neotropical birds, (2) hummingbird pollination, (3) bird life-histories, and (4) mistletoe dispersal (Appendix 1). This compilation is useful in identifying general trends and documenting the diversity of birds that use epiphytes. The extent to which this summary can be generalized to a community level is limited, however, as it reflects the purposes and geographical locations of studies not specifically designed to assess the importance of epiphytes to birds.

A total of 193 species of birds in 125 genera and 25 families has been cited as using epiphytes (Appendix 1). Birds of the three major diet categories (frugivores, insectivores, and nectarivores) are represented in approximately equal proportions. Bird families most frequently cited as users of epiphytes are the Thraupidae (tanagers) and Trochilidae (hummingbirds), 52 and 37 species, respectively. Other major bird families that use epiphyte resources are Furnariidae (ovenbirds, 14 species), Tyrannidae (flycatchers, 14 species), Fringillidae (finches, 8 species), Parulidae (warblers, 8 species), and Turdidae (thrushes, 7 species). Nesting materials from epiphytes have been noted anecdotally for many species of birds, and are most commonly collected by Furnariidae.

Epiphyte resources used by birds include fruits, flowers, seeds, water, and invertebrates in bromeliad "ponds" and sequestered in dead organic matter beneath moss mats, nesting materials, and nest sites. The most frequent citations concerned foraging for epiphytic fruits and nectar in flowers (Table 1 and Appendix 1). The list of epiphytes used by birds includes 42 genera in 15 families of vascular and nonvascular plants (Table 1). The Bromeliaceae, Loranthaceae, Marcgraviaceae, and Ericaceae are the families of vascular epiphytes most frequently cited for use by birds.

FIELD STUDY OF EPIPHYTE USE BY BIRDS

STUDY AREA

Study sites were in Monteverde, Puntarenas Province, Costa Rica (10°18'N, 84°48'W). The area is a mosaic of primary lower montane wet forest and pastures of various land-use histories (Lawton and Dryer 1980). The bird community of Monteverde has been well studied, and bird-plant interactions have received particular attention (e.g., Wheelwright et al. 1984, Feinsinger et al. 1987). We selected 14 sites between 1,350 and 1,420 m in elevation and within 2 km of each other. These sites represent the range of habitats in the area: (a) three sites in primary lower montane forest, (b) five sites in "relict tree pastures" (pastures partially cut, leaving some primary forest trees), and (c) six sites in "scrub tree pastures" (pastures cut completely, with a similar density of second-growth tree species colonizing the pastures). Differences in bird use of epiphytes in the three habitats will be described elsewhere (Nadkarni and Matelson, unpubl.)

Epiphytes of the Monteverde community are described in Nadkarni (1986). The taxonomy and distribution of epiphytes are in general only poorly known, and no quantitative assessment of epiphyte abundance in particular habitats or on individual trees in Monteverde are currently available. We categorized the diverse community of epiphytes into six groups: (1) woody shrubs—mainly species of *Cavendishia, Gonocalyx, Dys-*

TABLE 1. Bird use of epiphytes by plant group and resource type, based on information from 55 published reports. A total of 193 bird species have been recorded to use epiphytes. Epiphyte resource type: In = invertebrates; Fl = flowers (mainly nectar); Fr = fruits or seeds; Ne = nesting material, nest sites, or nest cover; Wa = water.

Number of bird species using epiphytes	Plant group	Resource type
58	Bromeliacae	In Fl Fr Wa Ne
53	Bryophyta	In N Wa
50	Loranthaceae	Fl Fr
39	Marcgraviaceae	In Fl Fr
18	Ericaceae	Fl Fr Ne
12	Gesneriaceae	Fl Fr
9	Guttiferae	Fl Fr
8	Solanaceae	Fr
6	Araceae	Fr Ne
6	Araliaceae	Fr
5	Lichens	In Ne
5	Orchidaceae	Fr Ne
5	Cactaceae	Fr
3	Pteridophyta	Ne
1	Begoniaceae	Ne
1	Piperaceae	Ne
1	Rubiaceae	Fr

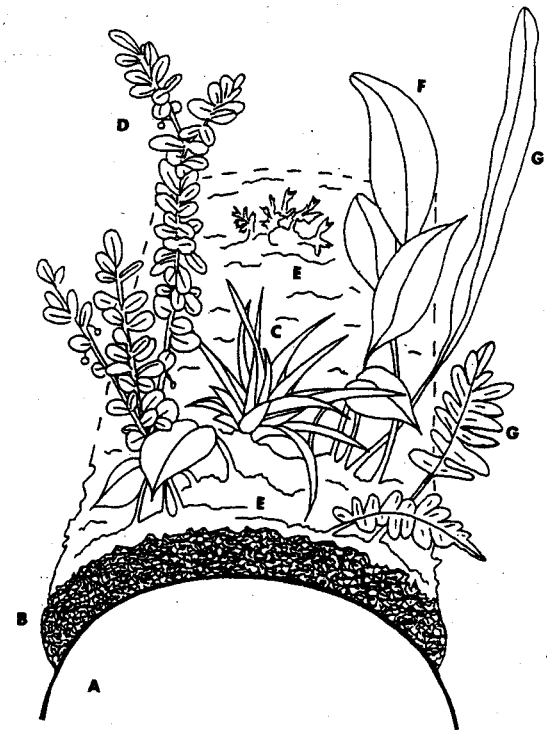

FIGURE 1. Epiphyte mat. A = branch, B = dead organic matter, C = bromeliads, D = ericaceous shrub (woody shrub), E = mosses and filmy ferns, F = orchid (herbaceous plants), G = ferns.

terigma, and *Satyria* (Ericaceae), *Lycianthes synthera* (Solanaceae), *Hillea* spp. (Rubiaceae), *Norantea costaricensis* (Marcgraviaceae), *Clusia* spp. (Guttiferae), and *Didymopanax* sp. (Araliaceae): (2) tank bromeliads—species of *Tillandsia, Guzmania,* and *Vriesia* (Bromeliaceae); (3) herbaceous epiphytes—species of the Orchidaceae, Begoniaceae, Gesneriaceae, Araceae, Cactaceae, *Peperomia* (Piperaceae), and ferns; (4) mistletoes (Loranthaceae) (although they are not true epiphytes, they are included as they provide canopy resources distinct from host trees); (5) dead organic matter, lichens, mosses, and other cryptogams which make up interwoven moss-root-humus mats of "crown humus" (Jenik 1973); and (6) other epiphytes—unknown vascular and nonvascular plants (Fig. 1). In general, forest and relict pasture tree-crowns supported large amounts of cryptogams and dead organic matter, woody shrubs, and herbs; epiphyte communities in scrub pastures were dominated by xerophytic shrubs and herbs, mistletoes, and tank bromeliads (pers. observ.).

METHODS OF OBSERVATIONS

Observations of bird activities were carried out daily from 1 July to 28 August 1985 by three observers familiar with resident birds and the vegetation of the area. At each of the 14 sites, we established a semicircular observation arena, approximately 30 m in radius, that contained nine to 17 trees ($\bar{x}$ = 12, SD = 5.1). Separate observers recorded bird activities in forest and pasture sites simultaneously. Observation sessions, distributed evenly throughout the study period, were 3 hr long, with two sessions per day, between 06:00 and 18:00, as weather permitted. The total amount of observation time in forest and pasture (relict plus scrub pasture) sites was nearly equal (140 and 149 hr, respectively), and all direct comparisons have been corrected for the discrepancy (3%) in observation time.

In forest sites two observers were needed. One watched understory birds by walking around the periphery of the arena on the ground. Another observer, suspended on a portable platform 25 m above the forest floor (Nadkarni 1988), recorded birds in the canopy. Tree-climbing methods followed those of Perry (1978). Our presence in the canopy did not appear to affect bird be-

havior, because birds perched, vocalized, and foraged on branches within 1 m of the platform. In pasture sites, a single observer on the ground had an unobstructed view of the entire arena.

We recorded the number of birds that alighted on trees in our sites, and noted whether they perched, vocalized, or foraged. In this paper, we discuss only those visits that involved foraging activities of birds in trees or epiphytes. The "visit," our unit of epiphyte or host tree use, was defined as an individual bird exhibiting any of the foraging behaviors (following Remsen and Robinson, unpubl.) listed below for more than 2 sec. For each visit, we noted bird species, whether it used a host tree or an epiphyte (and, for the latter, epiphyte group used), and foraging behaviors: (1) collecting or consuming fruit, (2) probing flowers or hovering at extrafloral nectaries for nectar, water, or invertebrates, (3) gleaning foliage for invertebrates, (4) probing moss mats and crown humus for invertebrates or water, (5) probing bromeliad tanks for invertebrates or water, and (6) general searching behavior that resulted in no immediate use or removal of material. The latter category was somewhat subjective, but we distinguished general searching behavior from other uses if there was no bill contact with the substrate. General searching was distinguished from mere perching if birds exhibited behaviors that we recognized as preceding a collecting or feeding event such as hovering, hopping near, or closely observing fruit, flowers, extrafloral nectaries, or bark crevices. Bird nomenclature generally follows Meyer de Schauensee (1970) and the AOU check-list (1983).

RESULTS

Seventy-one species of birds visited our sites during the study period. Of the 56 bird species that foraged in our sites, 33 species (59%) used epiphytic resources. We are confident that our observations encompassed the true composition of the bird community during the study period, because we observed 37 of the total 56 species by the end of the first 30 days of the study, and only four additional species were recorded between day 40 and the end of the 60-day study.

We recorded a total of 3,473 visits (perching, vocalizing, and foraging), of which 1,935 (56%) involved foraging behavior. Overall, 620 (32%) of these foraging visits involved epiphyte use. The proportion of epiphyte visits relative to host tree visits varied with bird species (Table 2). Bird species that used epiphyte resources most frequently were hummingbirds, tanagers, and flycatchers. Birds which were seen in our sites and which did not use epiphytes are listed in Appendix 2.

The foraging behaviors associated with epiphytic resources differed from behaviors associated with host tree resources (Fig. 2). Thirty percent of the epiphyte visits involved specialized epiphyte foraging behaviors (probing in moss mats and probing bromeliads for water or invertebrates) that have no host tree counterpart. For the four other foraging categories, the proportions differed significantly, using contingency table analysis ($\chi^2 = 70.7$, df = 3, $P < 0.001$); proportionately, birds foraged more frequently on epiphyte flowers than on host tree flowers. A greater proportion of foraging visits was spent in general searching (no immediate food acquisition) in host trees than in epiphytes.

The most commonly used epiphyte type was woody shrubs, and the least common was herbaceous epiphytes (Fig. 3). Of the birds that used epiphytes frequently (Table 2), some appeared to forage preferentially in particular epiphyte types. We used contingency table analysis to test whether the relative proportions of epiphyte types used by each of these species differed from the proportions used by all species combined. (We subtracted the visits of the species in question from the total). Five species differed significantly ($P < 0.01$) from the bird community as a whole in the relative proportions of epiphyte groups used (Fig. 3). The White-throated Mountain-gem used flowers of ericaceous shrubs significantly more frequently than expected; the Ochraceous Wren and Common Bush-Tanager foraged in dead organic matter and mosses more frequently, and the Golden-browed Chlorophonia and Olive-striped Flycatcher fed on mistletoes more frequently than expected.

Because our field season spanned only 2 months, we cannot ascertain if any birds specialized on epiphytes over host tree resources during the entire year. However, two species of birds exhibited almost exclusive use of a single epiphyte type during the study: the Variable Mountain-gem used woody shrubs, and the Ochraceous Wren foraged in dead organic matter for over 90% of their epiphyte visits. These two bird species had the highest proportion of epi-

phyte visits of all bird species (97% and 89% of all foraging visits, respectively, Table 2).

Seven species of birds appeared to specialize on particular types of epiphytes; i.e., even if they did not use epiphytes as the major part of their total resource use, over 90% of their epiphyte visits involved particular epiphyte types (Table 3A). Five other species were considered epiphyte generalists, using at least four of the five epiphyte types, with no more than 40% in any one category (Table 3B).

Specialization at a fine spatial scale occurred for one genus of epiphyte, which was used in a variety of ways by six bird species. In one of our forest sites, a woody epiphytic shrub, *Norantea* sp., (Marcgraviaceae) covered approximately 5 m of a horizontal *Dussia* sp. (Leguminoseae) tree branch (diameter = 25–30 cm) 23 m above the forest floor. We estimated that the shrub held between 300 and 350 fruits that ripened throughout our study period, turning from light green to red in color. We observed six species of birds using the shrub: Slate-throated Redstarts gleaned its foliage; Silver-throated Tanagers and Emerald Toucanets fed upon its fruits; Stripe-tailed Hummingbirds and Variable Mountain-gems visited extrafloral nectaries; and Prong-billed Barbets gleaned branches.

DISCUSSION

Our literature search and field observations summarize what is currently known about the use of epiphytes by tropical birds. Patterns described for the larger geographical areas encompassed in the literature were consistent with results from the montane landscape of Monteverde. A diverse assemblage of birds use epiphyte-derived resources when foraging for nutrients, energy, water, and nesting materials.

If the proportion of foraging visits to a resource is a general indicator of its importance to birds, our results suggest that the total resource pool available to birds in tropical forests is underestimated if epiphyte resources are discounted or only qualitatively described. One-third of all visits that we classified as foraging involved resources created by epiphytes. The actual resources obtained from epiphytes may be even greater compared to those obtained from host trees, because a larger proportion of tree visits were "general searching," a behavior that resulted in no immediate reward. However, since the chance of prey acquisition by such behaviors as probing into moss mats and bromeliad tanks is unknown, the size of this underestimation cannot be quantified with these data.

This potential underestimation of total resources available and used by birds has only infrequently been considered in discussions of the latitudinal gradient of bird diversity. The greater diversity of birds in tropical vs. temperate forests has been attributed to various aspects of habitat diversity and resource availability (MacArthur and MacArthur 1961; Orians 1969; Karr 1971, 1975; Karr and Roth 1971; Lovejoy 1971; Recher 1971; Terborgh 1971; Stiles 1985). The higher diversity in tropical forests has most often been linked to the greater complexity of tropical forest structure, particularly with structural indices such as foliage height diversity (MacArthur and MacArthur 1961; Terborgh and Weske 1969; Karr 1971; Pearson 1971, 1977; Recher 1971; Willson 1974). Another factor to explain higher tropical bird diversity is the presence of certain resource elements in tropical forests that have no counterpart in temperate forests. Examples of "new resources" (Karr 1975) that are exploitable in tropical but not temperate forests and that enhance particular bird species or guilds of bird species include large insects (Schoener 1971), army ants (Willis and Oniki 1978), bamboo thickets (Parker 1982), oxbow lake edge and permanently flooded forest (Remsen and Parker 1983), and suspended dead leaves (Remsen and Parker 1984).

An abundant epiphyte community contributes both to the vertical structural diversity of forest vegetation and to the amounts and types of food and energy resources available to animals. We suggest two mechanisms by which epiphytes might maintain or enhance bird species diversity at the community level: (1) epiphytes swell the canopy resource pool by producing additional resources that are "auxiliary" to those created by host trees, and which may enhance opportunities for resource specialization, and (2) phenological differences between epiphytes and their hosts make some epiphyte resources available to birds at a different time of the year than those provided by host trees.

MECHANISM 1: PRODUCTION OF AUXILIARY RESOURCES

In moist and wet tropical forests, epiphyte species constitute 34% to 63% of all plant species (Gentry and Dodson 1987). Their diverse growth-

TABLE 2. Percentage of foraging visits to epiphytes by birds in the Monteverde field study, 1 July to 28 August 1985. Frequent foragers had 10 or more foraging visits recorded during the study period. Infrequent foragers had less than 10 foraging visits recorded. Foraging behavior (in descending order of frequency of use): B = probing bromeliads, Dm = probing moss mats and dead organic matter, Fg = gleaning foliar and stem surfaces, Fl = probing or hovering at flowers or extrafloral nectaries, Fr = gathering or consuming fruit, Gs = general searching with no immediate resource use.

Bird species	% (Total number) foraging visits to epiphytes	Foraging behavior
Frequent foraging visits (>10 foraging visits)		
White-throated Mountain-gem *Lampornis castaneoventris*	95 (150)	Fl Gs Dm Fr Fg
Ochraceous Wren *Troglodytes ochraceus*	89 (19)	Dm B Fl
Stripe-tailed Hummingbird *Eupherusa eximia*	71 (14)	Fl Fg
Common Bush-Tanager *Chlorospingus ophthalmicus*	57 (511)	Dm Fl Fg Fr Gs B
Olive-striped Flycatcher *Mionectes olivaceus*	46 (37)	Fr Fl Gs Fg Dm
Slate-throated Redstart *Myioborus miniatus*	45 (47)	Fg Dm Gs Fl
Yellow-throated Brush-Finch *Atlapetes gutturalis*	31 (13)	Fg
Prong-billed Barbet *Semnornis frantzii*	30 (23)	Fr Fl Gs Dm
Golden-browed Chlorophonia *Chlorophonia callophrys*	33 (187)	Fr Dm Gs B
House Wren *Troglodytes aedon*	26 (57)	Dm B Gs Fg Fr
Three-striped Warbler *Basileuterus tristriatus*	20 (10)	Dm
Paltry Tyrannulet *Zimmerius vilissimus*	15 (61)	Gs Fg
Scarlet-thighed Dacnis *Dacnis venusta*	14 (256)	B Fr Fl
Silver-throated Tanager *Tangara icterocephala*	13 (78)	Fl Fr
Yellow-throated Euphonia *Euphonia hirundinacea*	13 (16)	Fg
Fork-tailed Emerald *Chlorostilbon canivetii*	10 (20)	Fl
Brown-capped Vireo *Vireo leucophrys*	<10 (13)	Gs
Emerald Toucanet *Aulacorhynchus prasinus*	<10 (93)	Fr
Mountain Elaenia *Elaenia frantzii*	<10 (30)	Gs
Mountain Robin *Turdus plebejus*	<10 (146)	B Dm
Dusky-capped Flycatcher *Myiarchus tuberculifer*	<10 (50)	B
Infrequent foragers (<10 total foraging visits)		
Boat-billed Flycatcher *Megarynchus pitangua*		Fg
Orange-bellied Trogon *Trogon aurantiiventris*		B
Brown Jay *Cyanocorax morio*		B
Spotted Barbtail *Premnoplex brunnescens*		Dm
Coppery-headed Emerald *Elvira cupreiceps*		Fl

TABLE 2. Continued.

Bird species	% (Total number) foraging visits to epiphytes	Foraging behavior
Green-crowned Brilliant *Heliodoxa jacula*		Dm
Hepatic Tanager *Piranga flava*		Dm
Black-faced Solitaire *Myadestes melanops*		Gs
Sooty-capped Bush-Tanager *Chlorospingus pileatus*		B
Tufted Flycatcher *Mitrephanes phaeocercus*		Gs
Violet Sabrewing *Campylopterus hemileucurus*		Fl
White-eared Ground-Sparrow *Melozone leucotis*		Dm
All species	32 (1,935)	

forms increase the spatial complexity of tree crowns. Their live and dead components create microhabitats that support communities of invertebrates and vertebrates that do not exist in trees and forests devoid of epiphytes. Bromeliad tanks that impound water and litter and support animals are used by at least 58 species of birds (Table 1, Appendix 1). Forty-four bird species forage for invertebrates in crown humus contained in neotropical forest trees (Appendix 1).

Structurally and taxonomically diverse habitats also provide greater opportunities for resource subdivision and therefore greater bird diversity in many habitats (Orians 1969, MacArthur 1970, Cody 1974, Karr 1975). In our study, four of the 56 species foraging in our sites (7%) used epiphytes for more than 50% of their foraging (Table 2). This is similar to Remsen's (1985) data from Bolivia, where four of the 80 montane bird species (5%) are epiphyte specialists. These ideas concur with those of Remsen and Parker (1984), who documented guilds of as many as eight sympatric bird species that forage

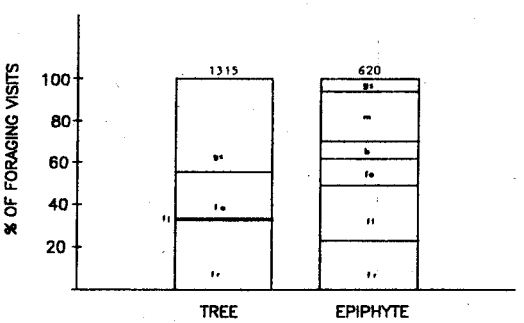

FIGURE 2. Foraging behavior of birds associated with tree and epiphyte resources during the study period. fr = collecting and/or consuming fruit; fl = probing or hovering at flowers or extrafloral nectaries; fo = gleaning foliage; b = probing bromeliad tanks and leaf bases; m = probing moss mats and crown humus; gs = general search with no immediate use or removal of material. Total number of foraging visits is shown above each bar.

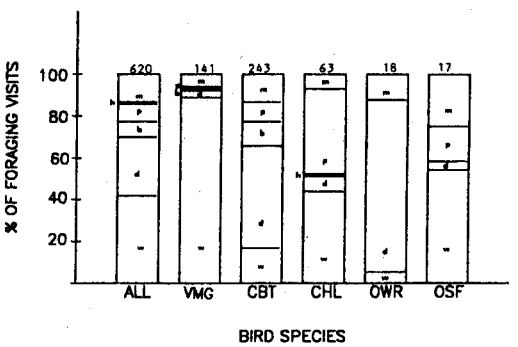

FIGURE 3. Bird use of the six epiphyte types in Monteverde during the study period. The six bird species presented are the most common species that used epiphytes for at least 30% of their total foraging visits and that differed significantly from the overall bird community in the proportion of types of epiphytes used. VMG = White-throated Mountain-gem (*Lampornis castaneoventris*); CBT = Common Bush-Tanager (*Chlorospingus ophthalmicus*); CHL = Golden-browed Chlorophonia (*Chlorophonia callophrys*); OWR = Ochraceous Wren (*Troglodytes ochraceus*); OSF = Olive-striped Flycatcher (*Mionectes olivaceus*). Epiphyte types are described in the text: w = woody shrubs; d = dead organic matter and mosses; b = bromeliads; p = parasites and mistletoes; h = herbaceous epiphytes; m = miscellaneous and unidentified epiphytes.

TABLE 3. Bird species exhibiting (A) specialized and (B) generalized use of the five types of epiphytes described in the text. Only those species with more than five visits are presented. (A) Specialists used the indicated epiphyte type for 90% or more of their epiphyte visits. (B) Epiphyte generalists used at least four epiphyte types in similar proportions (no one epiphyte type exceeded 40% of total use).

Epiphyte type	Bird species
A. Specialists	
Woody shrubs	White-throated Mountain-gem
	Emerald Toucanet
	Silver-throated Tanager
	Three-striped Warbler
Moss mats and crown humus	Ochraceous Wren
	Spotted Barbtail[1]
Bromeliads	Brown Jay[1]
B. Generalists	
Golden-browed Chlorophonia	Prong-billed Barbet
Paltry Tyrannulet	House Wren
Common Bush-Tanager	

[1] Based on <10 foraging observations.

on the invertebrates in suspended dead leaf clusters of South American forests. They proposed that this resource, which occurs on a year-round basis almost exclusively in tropical forests, enhances both the resource base of the forest and the potential for specialization, which would increase species diversity. The pool of epiphyte resources and the degree of preferential use we describe for a Costa Rican landscape may function in the same way.

MECHANISM 2: TEMPORAL PARTITIONING OF RESOURCES

Many tropical forests are subject to major seasonal fluctuations in production of food resources, and some frugivores switch to other "keystone plant resources" such as flowers, foliage, and sap when fruits are rare (Terborgh 1986, Terborgh and Stern 1987). Although these foods may be of poor nutritional quality, they are important to the frugivore community, because they tide the animals over an otherwise unfavorable time of year. Although few quantitative data on epiphyte phenology at the community level exist, some epiphytes differ in phenology compared to host trees (Croat 1975, Feinsinger et al. 1987). During our field study period, only seven of the 44 trees in our three forest interior sites were in fruit or flower. However, many of the woody epiphytic shrubs (including the *Norantea* described above) were in flower or fruit and were used for 40% of all foraging visits (Fig. 3).

The volume and biomass of epiphytes, then, may be far smaller than host trees, but the timing of their resources may differ in crucial ways. We propose two temporal effects that could maintain or enhance bird species diversity in forests with well-developed epiphyte communities. First, epiphytic resources may function as supplements during "lean times" of trees and understory plants, producing flowers, fruits, and leaves continuously (or asynchronously) throughout the year. Second, certain epiphytes such as mosses, bromeliad tanks, and canopy humus may provide microhabitats for invertebrates, which appear to be less seasonal than habitats provided by the canopy tree alone.

Epiphytic communities occur in a wide range of tropical forests and in some temperate forests (Nadkarni 1985, Gentry and Dodson 1987) and vary among forest types with respect to species richness, structure, and other community characteristics. In which forest types might we expect epiphytes to have a strong influence on bird community ecology? The epiphytes in temperate rain forests that are comparable in biomass to the epiphytes of tropical montane forests (Nadkarni 1985) consist exclusively of nonvascular and lower vascular plants, and thus do not provide the rich flower and fruit resources used frequently by frugivorous and nectarivorous birds. We could find no data on insectivorous bird use of invertebrates living in canopy humus of temperate wet forests.

Epiphytes are found in nearly all tropical forests, but their composition and biomass varies greatly among habitats. The most striking distributional pattern of epiphytes is a dramatic decrease in the number of epiphyte species and individuals in dry habitats (Gentry and Dodson 1987). Even in the driest habitats, however, orchids, cacti, bromeliads, and ferns can be found and may provide important arboreal resources, especially when their deciduous host trees are leafless. Lowland wet tropical forests are extremely rich in terms of epiphyte diversity, and are dominated by hemi-epiphytes, aroids, bromeliads, and woody shrubs. However, they tend to lack the contiguous moss mats of montane forests that foster accumulations of dead organic

matter (Gentry and Dodson 1987). In contrast, tropical elfin forest trees are covered with large loads of cryptogams and associated crown humus, but lack the angiosperm component that would provide a large resource base for frugivorous and nectarivorous birds. Neotropical mid-elevation forests (2,000–2,500 m in the Andes and 1,800–2,100 m in Central America) support the greatest taxonomic and structural diversity of epiphytes of any forest type (Madison 1977), and the epiphyte community in those habitats would most strongly enhance bird diversity.

If structural diversity and new resources are important components of increased bird diversity in the tropics, then species diversity of birds using epiphytes (percent use, specialization, etc.) should increase along the same gradients of increased epiphytic plant diversity in tropical forests. In fact, some data by Orians (1969) and Terborgh (1975) suggest that this might be true. The available information on bird-epiphyte relationships indicates the potential importance of epiphytes to certain tropical birds, but determination of how they influence the avifauna as a whole awaits further investigation. Quantitative information is needed on the relative nutritional and energy values of epiphyte vs. host tree resources, the quantities and phenology of epiphytic resources available to birds relative to host trees, and the abundance and availability of invertebrates dwelling in epiphyte-created microhabitats. Time-based studies focusing on the behavior of birds will be crucial to determine the importance of epiphytes to birds. Because our field season coincided with the North American summer, epiphyte use by temperate migrants remains unknown.

Researchers addressing these questions should note that gathering information from observation positions within the canopy greatly enhanced our ability to discriminate between the sources and types of resources used by birds. The degree of specialization on resources within the canopy and even on single plants (as in the case of *Norantea*) would be impossible to discern if observations were made from the ground. As canopy equipment becomes more widely used, more questions concerning the interactions of canopy plants and animals can be addressed.

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APPENDIX 1. Bird use of epiphytes, compiled from 55 published studies. Epiphyte resource type: Fl = Flowers (mainly nectar); Fo = General foraging; F Fruits; In = Invertebrates; Ne = Nesting material, nest sites, or nest cover; Se = seeds; Un = Unknown; Wa = Water. Epiphyte taxon: Ar = Aroids; B = Bromeli Be = Begoniaceae; C = *Clusia* spp.; E = Ericaceous shrubs; F = ferns; G = General epiphyte mats, encompassing a variety of unidentified species; Gu = Guttife Ma = Marcgraviaceae; Mi = mistletoes; Mo = mosses and bryophytes; O = Orchidaceae; R = Rubiaceae; So = Solanaceae; Un = Unknown.

Bird family	Genus	Species	Resource	Epiphyte taxon	Source
Accipitridae	*Spizaetus*	*ornatus*	Ne	B	14
Cracidae	*Chamaepetes*	*unicolor*	Se	Ar	12
Columbidae	*Columba*	*fasciata*	Fr	Mi	38
	Columba	*flavirostris*	Fr, Ne	Mi, U	38
	Columba	*nigrirostris*	Fr	Mi	13
Cuculidae	*Piaya*	*cayana*	Ne	B	38
Trochilidae	*Doryfera*	*ludoviciae*	Fl, Ne	B, E	55
	Glaucis	*hirsuta*	Fl	B, Ma	42
	Phaethornis	*guy*	Fl	B, E, G, Ma, R	42, 55
	Phaethornis	*superciliosus*	Un	G	50
	Phaethornis	*eurynome*	Fl	B	1
	Phaethornis	*longuemareus (adolphi)*	Fl	B	42
	Campylopterus	*curvipennis*	Fl	B	50
	Eupetomena	*macroura*	Fl	B	1
	Florisuga	*mellivora*	Fl	Ma	42
	Colibri	*delphinae*	Fl	E, G, Gu, Ma	55
	Colibri	*thalassinus*	Fl	B, E, Mi, Un	39, 55
	Anthracothorax	*nigricollis*	Fl	Ma	42
	Anthracothorax	*mango*	Fl	B	9
	Abeillia	*abellei*	In	Mo	51
	Popelairia	*conversii*	Fl	Gu, Ma	55
	Chlorestes	*notatus*	Fl	Ma	42
	Chlorostilbon	*aureoventris*	Ne	B	8
	Thalurania	*colombica*	Fl	O	37
	Panterpe	*insignis*	Fl, Fo, Un	B, E, Mi, Un	5, 15, 39, 46, 5
	Trochilius	*polytmus*	Fl	B, G, Ma	9
	Leucochloris	*albicollis*	Fl	B	1
	Amazilia	*candida*	Fl	B, Mi	50
	Amazilia	*chionopectus*	Fl	B, Ma	42
	Amazilia	*cyanifrons*	Fl	B	43
	Amazilia	*tobaci*	Fl	B, Ma	42
	Amazilia	*yucatanensis*	Fl	B	50
	Amazilia	*tzacatl*	Fl, Wa, Un	B, Ma, Mo, So	32, 37, 50
	Eupherusa	*nigriventris*	Fl	B, E, G, Gu, Ma, O	55
	Elvira	*cupreiceps*	Fl	B, E, Gu, Ma, O	55
	Lampornis	*amethystinus*	In	Mo	51
	Lampornis	*hemileucus*	Fl	B, E, G, Gu, Ma, O	55

APPENDIX 1. Continued.

Bird family	Genus	Species	Resource	Epiphyte taxon	Source
	Lampornis	*castaneoventris*	Fl	B, E, G	55
	Heliodoxa	*jacula*	Fl	B, E, Ma	55
	Eugenes	*fulgens*	Fl	B, E	55
	Coeligena	*prunellei*	Fl	B	43
	Mellisuga	*minima*	Fl	B	9
	Selasphorus	*flammula*	Fl	B, E, Mi	55
	Non-hermit		Fl	B, G, E	45
	Hermit		Fl	B, G, E	45
Trogonidae	*Trogon*	*aurantiiventris*	Fr, Ne	E, Un	38, 54
	Trogon	*violaceus*	Ne	Un	37
Capitonidae	*Capito*	*maculicoronatus*	Ne	Mo	34
	Semnornis	*frantzii*	Fr, Ne	Ar, Ma, U	36, 38
Ramphastidae	*Aulacorhynchus*	*prasinus*	Fr, Ne, Se	Ar, Ma, So	12, 36, 38, 54
	Petroglossus	*frantzii*	Fr	Ma	36
Picidae	*Melanerpes*	*radiolatus*	Fo	Un	9
	Melanerpes	*rubricapillus*	Fr	Ma	36
	Centurus	*pucherani*	Fo, Wa	Mo, Un	39
	Piculus	*rubiginosus*	Fo	Mo	39
	Piculus	*rivolii*	Fo	Mo	29
	Piculus	*simples*	Fo	Un	37
Dendrocolaptidae	*Dendrocincla*	*homochroa*	Fo	Mo	39
	Xiphorhynchus	*guttatus*	In	Mo, So	37
	Lepidocolaptes	*affinis*	Fo	Mo	29
Furnariidae	*Synallaxis*	*gularis*	Fo	Mo	23
	Cranioleuca	*erythrops*	Fo, In	Un	25, 39
	Cranioleuca	*vulpina*	In	Un	26
	Cranioleuca	*marcapatae*	Fo	Mo, B	20
	Cranioleuca	*albiceps*	Fo	Mo	29
	Cranioleuca	*albicapilla*	Fo	Mo, B	20
	Schizoeaca	*harterti*	Fo	Mo	29
	Asthenes	*urubambensis*	Fo, In	Mo	20
	Siptornis	*striaticollis*	Fo	Mo	5
	Margarornis	*bellulus*	Fo	B, Mo	31
	Premnoplex	*brunnescens*	Fo, In	Mo, Un	27, 39
	Pseudocolaptes	*lawrencii*	Fo	Un	30
	Pseudocolaptes	*boissonneautii*	Fo	Mo, Un	20
	Syndactyla	*subalaris*	In	Un	25
	Automolus	*ruficollis*	Fo	B, F, Mo	23
	Thripadectes	*rufobrunneus*	Fo	Un	39

APPENDIX 1. Continued.

Bird family	Genus	Species	Resource	Epiphyte taxon	Source
Formicariidae	*Cymbilaimus*	*lineatus*	Ne	F	34
	Dysithamnus	*striaticeps*	Ne	Mo	34
Cotingidae	*Zaratornis*	*stresemanni*	Fr	Mi	19
	Pipreola	*riefferii*	Ne	Mo	16
	Pachyramphus	*versicolor*	Ne	Mo	34
Pipridae	*Pipra*	*coronata*	Fr	Ma	36
	Chiroxiphia	*linearis*	Fr	G	54
	Manacus	*vitellinus*	Fr	Mi	13
	Tyranneutes	*stolzmanni*	Fr	Un	24
	Piprites	*chloris*	Fr	Un	24
Tyrannidae	*Myiotheretes*	*fumigatus*	Fo, In	Mo, Un	20
	Myiozetetes	*similis*	Fr	Mi	13
	Attila	*spadiceus*	Ne	B, Be, Un	37
	Contopus	*lugubris*	Ne	Mo	34
	Empidonax	*flavescens*	Ne	Mo	34
	Mitrephanes	*phaeocercus*	Ne	Mo	34
	Myiopagis	*flavivertex*	Fr	Mi	9
	Lophotriccus	*pileatus*	Ne	Mo	34
	Mecocerculus	*stictopterus*	Fo	Mo	29
	Elainea	*frantzii*	Ne	Un	34
	Myiophobus	*fasciatus*	Ne	B	7
	Camptostoma	*obsoletum*	Ne	Mo, Un	37
	Phyllomyias	*uropygialis*	Fo	Mo	29
	Zimmerius	*vilissimus*	Fr	Mi	13
	Zimmerius	*bolivianus*	Fo	Mi	30
	Tyranniscus	*elatus*	Fr	Mi	13
	Mionectes	*olivaceus*	Fr	Mi	54
	Mionectes	*oleagineus*	Fr	Mi	13
Oxyruncidae	*Oxyruncus*	*cristatus (frater)*	Fo, Fr, In	E, Mi, Mo, Un	39, 48
Corvidae	*Cyanocitta*	*stelleri*	Fo	Mo	34
	Cyanolyca	*pumilo*	Fo	Un	34
	Psilorhinus	*morio*	Wa	B	11
Troglodytidae	*Odontorchilus*	*branickii*	Fo	Mo	22
	Troglodytes	*ochraceus*	Fo, In	Un	25, 39
	Troglodytes	*solstitialis*	Fo	Mo	29
	Henicorhina	*leucophrys*	In	Un	26
Turdidae	*Myadestes*	*melanops*	Fr, Ne	E, G, Ma, Mo, So	34, 54
	Myadestes	*obscurus*	Ne	O	34
	Myadestes	*ralloides*	Ne	Mo	16

APPENDIX 1. Continued.

Bird family	Genus	Species	Resource	Epiphyte taxon	Source
	Turdus	*serranus*	Ne	Mo	16
	Turdus	*plebejus*	Fo, Fr, Ne, Se	At, Ma, Un	12, 34, 54
	Turdus	*ignobilis*	Ne	Mo	16
	Turdus	*grayi*	Ne, Se	B, Gu, Ma, Mi, Un	17, 36, 37
Ptilogonatidae	*Ptilogonys*	*cinereus*	Fr, Ne	Mi, Mo, So	18, 33, 49
	Ptilogonys	*caudatus*	Fo, Ne	Mi, So	33
	Phainoptila	*melanoxantha*	Se	Ar	12
	Phainopepla	*nitens*	Fr	Mi	52
Vireonidae	*Cyclarhis*	*gujanensis*	Ne	E	34
Parulidae	*Mniotilta*	*varia*	In	B	10
	Vermivora	*gutturalis*	Ne	B	34
	Dendroica	*pharetra*	In	B	10
	Dendroica	*dominica*	In	B	10
	Dendroica	*tigrina*	In	B	10
	Helmitheros	*vermivorus*	In	B	10
	Myioborus	*miniatus*	Ne	Mo	16
	Myioborus	*melanocephalus*	Fo	Mo	29
Icteridae	*Psarocolius*	*wagleri*	Fo	Mo, Un	48
	Cacicus	*uropygialis*	Fo, In, Ne	Mo, Un	34, 36, 48
	Cacicus	*leucorhamphus*	Fo, In	Mo	29
	Icterus	*leucopteryx*	Fo	Un	9
	Nesopsar	*nigerrimus*	In	B, Mo, Un	3, 9
Thraupidae	*Dacnis*	*cayana*	Fr	Ma, Mi	36, 41
	Chlorophanes	*spiza*	Fl, Fr, In, Wa	B, Gu, Ma, Mi, So	36, 37, 41
	Cyanerpes	*lucidus*	Fo, Fr, Ne	Ma, Un	34, 36
	Cyanerpes	*caeruleus*	Fr	Mi	41
	Cyanerpes	*cyaneus*	Fr	Ma	36
	Diglossa	*cyanea*	Fo	Un	29
	Diglossa	*plumbea*	Fl, Fo	E, Un	39, 55
	Euneornis	*campestris*	Fl	B, G	9
	Conirostrum	*sitticolor*	Fo	Un	29
	Coereba	*flaveola*	Fr	C, Mi	41
	Chlorornis	*riefferii*	Fo	Mo	29
	Chlorospingus	*ophthalmicus*	Fr, In, Ne, Se	Ar, E, G, Mo, Un	12, 26, 34, 54
	Chlorospingus	*inornatus*	Fo	Mo	31
	Chlorospingus	*pileatus*	Se	Ar	12
	Chlorospingus	*canigularis*	Fo	Mo	21
	Hemispingus	*calophrys*	Fo	Mo	29
	Heterospingus	*rubrifrons*	Fr	Mi	13
	Tachyphonus	*luctuosus*	Fr	Ar	41

APPENDIX 1. Continued.

Bird family	Genus	Species	Resource	Epiphyte taxon	Source
	Tachyphonus	*rufus*	Fr	Ar, B, Mi	41
	Piranga	*bidentata*	Ne	Un	34
	Calochaetes	*coccineus*	Fo	Mo	21
	Ramphocelus	*carbo*	Fr	Ar, B	41
	Ramphocelus	*passerinii*	Fr	Ma, So	36, 37
	Thraupis	*episcopus* (*virens*)	Fo	Ma	36
	Thraupis	*palmarum*	Fr	C, Ma	36, 41
	Buthraupis	*montana*	Fo	Mo	29
	Dubusia	*castaneoventris*	Fo, In	Mo, B	20, 28, 29
	Euphonia	*jamaica*	Fr, Ne	B, Mi	9
	Euphonia	*affinis*	Fr	Mi	39, 49
	Euphonia	*luteicapilla*	Fr	Mi	39
	Euphonia	*violacea*	Fr	Ar, B, C, Mi	41
	Euphonia	*laniirostris*	Fr	Mi	39
	Euphonia	*hirundinacea* (*lauta*)	Fr	Mi	39, 49, 54
	Euphonia	*elegantissima*	Fr	Mi	16, 39, 49, 53
	Euphonia	*imitans*	Fo, Fr, Ne	F, Ma, So, Un	36
	Euphonia	*gouldi*	Fr	Mi	39
	Euphonia	*minuta*	Fo, Fr	Mi, Mo	34
	Euphonia	*rufiventris*	Fr	Un	24
	Chlorophonia	*callophrys*	Fr	Ma, Mi, So	54
	Tangara	*inornata*	Fr	Mi	13
	Tangara	*mexicana*	Fr	C, Mi	41
	Tangara	*chilensis*	Fr	Mi	2
	Tangara	*icterocephala*	Fo, Fr, In, Ne	Gu, Ma, Mo, So	36, 37, 39
	Tangara	*chrysotis*	Fo	Mo	21, 28
	Tangara	*guttata*	Fr	Ma	36
	Tangara	*gyrola*	Fr	Ma, Mi	36, 41
	Tangara	*larvata*	Fr, In, Se	Gu, Ma, Mi, Mo, So	13, 36, 37
	Tangara	*vassorii*	Fo	Mo	29
	Tangara	*callophrys*	Fo	Mo	39
	Tangara	*fucosa*	Fo	Mo, Un	31
Emberiadae	*Loxipasser*	*anoxanthus*	Fr	Mi	9
	Loxigilla	*violacea*	Fo, Fr	G, Mi	9
	Pinaroloxias	*inornata*	Fo	B	40
	Atlapetes	*rufinucha*	Fo	Mo	29
	Caryothraustes	*poliogaster*	Fr, Ne	B, C, Un	34
	Saltator	*maximus*	Fr	Ma	36
	Saltator	*albicollis*	Fr	Ma	36

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APPENDIX 2. Birds seen in study sites that did not use epiphytes.

Family	Scientific name	Common name
Cathartidae	*Cathartes aura*	Turkey Vulture
	Coragyps atratus	Black Vulture
Accipitridae	*Elanoides forficatus*	Swallow-tailed Kite
Falconidae	*Micrastur ruficollis*	Barred Forest-Falcon
Cracidae	*Chamaepetes unicolor*	Black Guan
Columbidae	*Columba fasciata*	Band-tailed Pigeon
	Columba subvinacea	Ruddy Pigeon
	Leptotila verreauxi	White-tipped Dove
Psittacidae	*Pionopsitta haematotis*	Brown-hooded Parrot
Cuculidae	*Piaya cayana*	Squirrel Cuckoo
	Crotophaga sulcirostris	Groove-billed Ani
Apodidae	*Streptoprocne zonaris*	White-collared Swift
	Chaetura vauxi	Vaux's Swift
Trochilidae	*Phaethornis guy*	Green Hermit
	Amazilia saucerottei	Steely-vented Hummingbird
Trogonidae	*Pharomachrus mocinno*	Resplendent Quetzal
	Trogon aurantiiventris	Orange-bellied Trogon
Momotidae	*Momotus momota*	Blue-crowned Motmot
Picidae	*Melanerpes hoffmanni*	Hoffmann's Woodpecker
	Piculus rubiginosus	Golden-olive Woodpecker
	Dryocopus lineatus	Lineated Woodpecker
	Campephilus guatemalensis	Pale-billed Woodpecker
Dendrocolaptidae	*Sittasomus griseicapillus*	Olivaceous Woodpecker
	Xiphocolaptes promeropirhynchus	Strong-billed Woodcreeper
	Xiphorhynchus erythropygius	Spotted Woodcreeper
Furnariidae	*Cranioleuca erythrops*	Red-faced Spinetail
	Thripadectes rufobrunneus	Streak-breasted Treehunter
Cotingidae	*Tityra semifasciata*	Masked Tityra
Tyrannidae	*Tyrannus melancholicus*	Tropical Kingbird
	Myiodynastes luteiventris	Sulphur-bellied Flycatcher
	Myiodynastes maculatus	Streaked Flycatcher
	Myiozetetes similis	Social Flycatcher
	Attila spadiceus	Bright-rumped Attila
	Elaenia chiriquensis	Lesser Elaenia
	Rhynchocyclus brevirostris	Eye-ringed Flatbill
Hirundinidae	*Notiochelidon cyanoleuca*	Blue-and-white Swallow
Corvidae	*Cyanolyca cucullata*	Azure-hooded Jay
Troglodytidae	*Henicorhina leucophrys*	Gray-breasted Wood-Wren
Turdidae	*Turdus grayi*	Clay-colored Robin
Vireonidae	*Hylophilus decurtatus*	Lesser Greenlet
Parulidae	*Dendroica fusca*	Blackburnian Warbler
	Basileuterus culicivorus	Golden-crowned Warbler
Icteridae	*Sturnella magna*	Eastern Meadowlark
Thraupidae	*Piranga flava*	Hepatic Tanager
	Thraupis episcopus	Blue-gray Tanager
	Euphonia anneae	Tawny-capped Euphonia
	Tangara dowii	Spangle-cheeked Tanager
Fringillidae	*Zonotrichia capensis*	Rufous-collared Sparrow
	Tiaris olivacea	Yellow-faced Grassquit