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UTILIZATION OF EPIPHYTES BY BIRDS IN A BRAZILIAN ATLANTIC FOREST

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Resumo. – O uso de plantas epífitas por aves na Mata Atlântica. – As plantas epífitas constituem grande parte da biomassa em florestas Neotropicais e podem oferecer elevada variedade de recursos para as aves. Considerando a importância estrutural e ecológica das plantas epífitas, existem poucos estudos que investigaram o uso de epífitas por aves na região Neotropical. No presente trabalho, estudamos o uso de plantas vasculares epífitas (e hemi-epífitas) por aves em uma região de Mata Atlântica no sudeste do Brasil. Os recursos explorados, a variação estacional na exploração no uso de epífitas, a freqüência de utilização e seletividade em epífitas e a relação entre a exploração de epífitas e a participação em bandos mistos foram investigados. Ao final de 360 h de observações foram registradas 24 espécies em um total de 74 interações de aves que exploraram epífitas. As famílias Thamnophilidae (quatro espécies), Trochilidae, Thraupidae e Furnariidae (três espécies cada) foram as mais representativas, enquanto Furnariidae e Dendrocolaptidae tiveram a maior freqüência de interações. Bromeliaceae e Araceae foram os grupos de plantas epífitas com maior abundância e as mais exploradas pelas aves. Néctar, água para consumo, material para construção de ninho e invertebrados foram os recursos mais explorados pelas aves, principalmente em Bromeliaceae. Não houve casos de especialização no forrageamento em epífitas ou seletividade em nenhum dos grupos de epífitas investigados. *Automolus leucophthalmus* (Furnariidae), espécie freqüentadora comum de bandos mistos de sub-bosque, explorou epífitas mais freqüentemente quando associada a estes bandos. O uso de epífitas foi oportunista pela maioria das espécies de aves e ocorreu durante o ano todo sem variação entre as estações chuvosa e seca.

Abstract. – Epiphytes constitute a great part of the vegetation biomass in Neotropical forests, offering a large variety of resources to birds. Despite their structural and ecological importance, few studies investigated the use of epiphytes by birds in the Neotropical region. We studied the bird species that exploit vascular epiphytes (and hemi-epiphytes) in an Atlantic forest site in southeastern Brazil. The resources exploited, seasonal variation in the use of epiphytes, the frequency of foraging and selectivity in epiphytes, and the relationship between the use of epiphytes and the participation in mixed-species bird flocks were investigated. After 360 h of observations along trails crossing the forest, 24 bird species (12 families) were recorded in a total of 74 events of epiphyte exploitation. Thamnophilidae (four species), Trochilidae, Thraupidae and Furnariidae (three species) were the richest bird families in our sample, while Furnariidae and Dendrocolaptidae were the more frequently recorded families. Plants in the Bromeliaceae and Araceae

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families were the most abundant and more frequently exploited epiphytes. Nectar, water, nest material and invertebrates were the most frequently exploited resources, mainly from Bromeliaceae. None of the species for which we had enough data revealed to be a frequent user of epiphytes for foraging or selective to any epiphyte group. The White-eyed Foliage-gleaner (*Automolus leucophthalmus*; Furnariidae), a common participant of understory mixed-species flocks, exploited epiphytes more frequently when associated with mixed-species flocks. The utilization of epiphytes was opportunistic for most of the bird species recorded and occurred throughout the year with no seasonal variation. *Accepted 29 October 2007*.

Key words: Atlantic forest, epiphytes, mixed-species flocks, foraging specialization.

INTRODUCTION

Epiphytes (*sensu lato*, including holo- and hemi-epiphytes, Gentry & Dodson 1987) are a prominent feature of tropical forests, where they may comprise up to 50% of the total vascular flora. Epiphytes are directly or indirectly responsible for a great part of the biotic diversity that makes tropical forest a complex terrestrial ecosystem (Benzing 1990, Nieder *et al.* 2001). Among the three big blocks of tropical forests in the world (i.e., Central and South America, Central Africa and Southeast of Asia), the greatest richness of epiphytes is found in the Americas, mainly in the Atlantic forest and humid forests of the Andes cordillera. Bromeliaceae, Orchidaceae, Araceae, Piperaceae and Gesneriaceae are the plant families that predominate as resources in the American tropics (Catharino & Barros 2004).

The abundance and diversity of epiphytes in tropical forests make them especially important resources, which may have influenced the diversity of birds in these forests, and suggest specialization in the exploitation of epiphytes by some bird species (MacArthur & MacArthur 1961, Nadkarni & Matelson 1989, Sillet 1994). In a direct way, epiphytes supply a variety of resources to birds, including nectar, fruits, seeds, nest material, nest sites, and water for consumption and bathing. Indirectly, epiphytes serve as micro-habitats for invertebrates and small vertebrates that constitute prey for many bird species. Nadkarni & Matelson (1989) suggested that epiphytes increase the resource availability for birds, frequently supplying food resources in periods of food scarcity.

A literature review based mostly on anecdotal observations scattered in the published ecological literature reported that 27 families and 193 species of birds use epiphytic resources in the Neotropical region (Nadkarni & Matelson 1989). Trochilidae (37 species), and Thraupidae (34) were the most frequent bird families recorded. Fruits and nesting material (including the use of epiphytes for nest placement and source of nest material) were the epiphytic most often utilized by birds.

Apart from sporadic observations and pollination studies involving epiphytes and hummingbirds (Sazima *et. al.* 1995, Buzato *et. al.* 2000, Machado & Semir 2006), there is a scarcity of knowledge regarding the use of epiphytes by birds in the Brazilian Atlantic forest, which is one of the most threatened biomes of the world, home of a great variety and abundance of epiphytes and endemic birds (Myers 1988, Brown & Brown 1992). In the only study conducted to date, Pizo (1994) recorded 24 bird species exploring epiphytic bromeliads in the Atlantic forest of southeastern Brazil. Members of Furnariidae, Thraupidae and Dendrocolaptidae searching for invertebrates constituted the bulk of the records in this study. At the same site, Rodrigues (1995) recorded five Thraupidae species searching for arthropods in epiphytes. The evidences available so far suggest that

some bird species, particularly in the families Furnariidae and Thraupidae, may specialize in the exploitation of food resources from epiphytes in the Atlantic forest, i.e., they would take most of their foods from epiphytes (Pizo 1994, Sick 1997)

In this study we investigated the utilization of epiphytes (and hemi-epiphytic Araceae) by birds in a well-preserved Atlantic forest site to answer the following questions: (i) which are the bird species that utilize epiphytic resources and the frequency of utilization? (ii) which epiphytes and epiphytic resources are most frequently exploited? (iii) is there any seasonal variation in the utilization of epiphytes by foraging birds? and (iv) do birds select a particular group of epiphytes to forage? Because mixed-species flocks of birds are a prominent feature of the Atlantic forest (Develey & Peres 2000), and the putative protection against predators provided by these flocks (Thiollay & Jullien 1998) may favor the careful and time-consuming inspection needed to capture arthropods amidst the leaves and roots of epiphytes, we also asked if the use of epiphytes for foraging is influenced by the participation in mixed-species flocks.

STUDY AREA AND METHODS

Study area. The study was conducted at Juréia-Itatins Ecological Station (JIES; 24°18'S, 47°00'W), located in the state of São Paulo, southeastern Brazil. With nearly 80,000 ha, JIES is one of the last blocks of well-preserved Atlantic forest. Climate is subtropical and humid, without a pronounced dry season. Mean annual rainfall is 2278 mm with the rainy season occurring from October to April, and the dry season from May to September (Tarifa 2004). Strong cold periods associated with polar masses are frequent during the autumn, winter and spring. Mean annual temperature is 21.4ºC, with maximum temperatures averaging 25.8ºC and minimum temperatures averaging 19.0ºC (Tarifa 2004). A total of 314 bird species (52 families) were recorded at JIES (Develey 2004). On the plant side, Mamede *et al.* (2004) found 630 species of flowering plants. The richest families of epiphytes and hemi-epiphytes are Orchidaceae (62 species), Bromeliaceae (20 species), Araceae (10 species), Cactaceae (7 species) and Gesneriaceae (5 species). A study of Pteridophyta revealed 86 species, although only some families (Dryopteridaceae, Grammitidaceae, Lomariopsidaceae, Lycopodiaceae) include epiphytic species (Prado 2004).

We searched for birds exploiting epiphytes along three 1-m wide trails totaling 4.2 km. Trail 1 (1.3 km) was located in Serra de Peruíbe, and trail 2 (1.5 km) was located near the Arpoador research base in Maciço de Paranapuã. The distance between these two trails is approximately 5.8 km, with an elevational gradient from 0 to 600 m a.s.l. Trail 3 (1.4 km) was established in the lowland forest near the Grajaúna research base at sea level. This trail, located 23 km and 27.5 km from trail 2 and trail 3, respectively, was the most remote trail with few human impacts.

Epiphyte exploitation. Trails were sampled monthly from January to December 2005. Each month, a different trail was sampled for a total of 30 h. Therefore, at the end of the study, we had 360 h of total observation (120 h in each trail). For all birds exploring epiphytes 1 m above the ground or higher, we recorded: (i) bird species (bird nomenclature follow CBRO (2006), (ii) epiphyte height (visually estimated), (iii) epiphyte group, (iv) the resources used, if any, and (v) if the bird was in a mixed-species flock or not. The bird species recorded were further classified into broad diet categories (i.e., foraging guilds: insectivorous, frugivorous, nectarivorous) based on personal observations and on the

TABLE 1. Records of birds exploiting epiphyte and non-epiphyte substrates with information on the epiphytes and resources exploited, forest strata and average height where epiphytes were exploited and diet categories of birds. Total at the end of the table refers to the total number of records including epiphytes and non-epiphytes substrates.

Species	N	Records in epiphytes (%)	Epiphyte group (number of records)[a]	Resources exploited (number of records)[b]	Forest strata (average height in m)[c]	Diet category[d]
Trochilidae						
Phaetornis rubber	13	1 (7.7%)	B (1)	Ne (1)	U (2)	N
Rhamphodon naevius	35	3 (8.5%)	B (3)	Ne (3)	U (2.8)	N
Thalurania glaucopis	44	1 (2.3%)	B (1)	Ne (1)	U (4.5)	N
Picidae						
Celeus flavescens	43	1 (2.3%)	B (1)	–	U (9)	I/F
Piculus flavigula	6	1 (16.6%)	B (1)	–	C (14)	I
Thamnophilidae						
Drymophila squamata	40	2 (5%)	A (1), P (1)	–	U (3.75)	I
Dysithamnus mentalis	39	1 (2.6%)	A (1)	–	U (4.5)	I
Dysithamnus stictothorax	14	1 (7.1%)	B (1)	–	U (4)	I
Myrmotherula minor	6	1 (16.6%)	A (1)	Art (1)	U (2.5)	I
Dendrocolaptidae						
Xiphocolaptes albicollis	6	2 (33.3%)	B (2)	–	U (1.75)	I
Xiphorhynchus fuscus	59	9 (15.2%)	B (8), A (1)	Art (1)[e]	U (6.7)	I
Furnariidae						
Automolus leucophthalmus	22	8 (36.3%)	B (2), A (6)	–	U (6.4)	I
Cichlocolaptes leucophrys	1	1 (100%)	B (1)	Spi (1)	C (12)	I
Phylidor atricapillus	39	16 (41%)	B (6), A (10)	Spi (1)[e]	U (5.5)	I
Tyrannidae						
Myiobius barbatus	30	2 (6.6%)	A (1), O (1)	–	U (3.75)	I
Troglodytidae						
Thryothorus longirostris	4	2 (50%)	B (2)	Art (1)	U (1.5)	I
Turdidae						
Platycichla flavipes	9	1 (11.1%)	B (1)	Wa (1)	C (10)	F/I
Thraupidae						
Habia rubica	53	2 (3.8%)	A (2)	–	U (3.5)	I/F
Tachyphonus cristatus	39	1 (2.6%)	B (1)	Ba (1)	U (3.5)	F/I
Tangara seledon	23	2 (8.7%)	B (2)	Nm (1)	U (5)	F/I
Parulidae						
Basileuterus culicivorus	143	7 (4.9%)	B (1), A (6)	–	U (3.8)	I
Icteridae						
Cacicus haemorrhous	19	1 (5.2%)	B (1)	–	C (10)	I/F
Fringillidae						
Euphonia pectoralis	35	7 (20%)	B (2), A (5)	Fr/Ne (1)[e]	U (5)	F
Euphonia violacea	15	1 (6.6%)	G (1)	–	C (15)	F
TOTAL	737	74				

[a]Epiphyte groups: B = Bromeliaceae, A = Araceae, P = Pteridophyta, O = Orchidaceae, G = Gesneriaceae.

[b]Resources exploited: Ne = nectar, Art = Arthropod, Spi = Spider, Wa = Water for drinking, Ba = Bathing, Nm = Nest material, and Fr = fruit.

[c]Forest strata: C = canopy (> 10 m heigh), U = understory (< 10 m heigh).

[d]Diet categories based on personal observations and on the literature (Moojen *et al.* 1941, Schubart *et al.* 1965, Willis 1979). Codes: (F) frugivorous, (I) insectivorous, (N) nectarivorous. When two codes were applied to the same bird species, the first code refers to the predominant diet category.

[e]*X. fuscus* captured the arthropod in a bromeliad; *P. atricapillus* captured the spider in an aroid, *E. pectoralis* exploited nectar in a bromeliad and fruit in an aroid.

literature (Moojen *et al.* 1941, Schubart *et al.* 1965, Willis 1979). Based on a previous survey of epiphytes in the area, epiphytes were divided into the following taxonomic categories: Bromeliaceae, Orchidaceae, Araceae, Gesneriaceae, Pteridophyta, and Cactaceae. The resources exploited were classified as: (i) fruits, (ii) flowers, (iii) nectar, (iv) invertebrates, (v) small vertebrates, (vi) nest materials (e.g., twigs, fibers, web spiders), (vii) nest site, (viii) water for drinking or (ix) bathing. A bird was considered exploiting an epiphyte every time it was actively inspecting, probing or removing resources from it. To guarantee independence among consecutive observations, only the first five seconds of substrate exploitation of each bird were observed (Hejl *et al.* 1990). If the bird changed substrate during the observation period, only the substrate exploited for longer time was considered. In the case of mono-specific flocks, only one individual was considered. For mixed-species flocks, we recorded data for one individual per species. When the observer clearly influenced the bird behavior, the record was not considered in the analyses.

The seasonal use of epiphytes as a source of food resources, the influence of the participation in mixed-species flocks on epiphyte foraging, and the frequency of foraging on epiphytes were investigated using the substrates exploited by birds for foraging. The seasonal use of epiphytes was tested with a log-likelihood ratio test (G-test) with Yates' correction (Sokal & Rohlf 1995) applied to a contingency table that contrasted the observed frequencies of epiphyte exploitation in the wet and dry seasons with the expected frequencies given by the null hypothesis of equal frequencies in both seasons. Because arthropods are especially sensitive to dry season weather conditions, when their abundances frequently drop thus potentially affecting insectivorous birds in particular (Davies 1945, Develey & Peres 2000), we made this seasonal analysis twice, considering all the bird species recorded and the insectivorous birds only. Fisher Exact tests (Sokal & Rohlf 1995) applied to each bird species were used to investigate the influence of the association with mixed-species flocks upon epiphyte foraging. For this, we used the records of the substrates used for foraging by birds (i.e., if epiphyte or non-epiphyte) when they were in and out of mixed-species flocks. To classify the birds in relation to the frequency of use of epiphytes for foraging, we followed the criterion adopted by Remsen & Parker III (1984), according to which the species of birds that foraged in epiphytes for more than 75% of records were considered frequent users, those for which between 25% and 75% of the records were epiphytes were regular users, whereas birds that foraged in epiphytes in less than 25% of the observations were considered occasional users. Only birds with more than five foraging records were classified in the above categories.

Epiphyte availability and foraging selectivity. The relative availability of each epiphyte category was calculated following the method outlined by Sillet (1994), which consists of recording the presence or absence of each epiphyte category in branches or any other woody tissue intersecting imaginary cylinders (1 m diameter) placed vertically from 1 m height to the canopy. For instance, if an imaginary cylinder intercepted four branches, and two of them had Bromeliaceae, this group of epiphyte was scored 0.5 (2/4). If other two branches had no epiphytes, the assigned score was 0.5 (2/4) for the category "absence of epiphytes". The availability of each group of epiphytes was then the total sum of the scores divided by the total number of cylinders. This proportion represents the probability of encountering a given group of epiphytes in a branch by chance. In the same way, the relative availability of a epiphyte group was estimated by calculating the proportion between its total score and the total score from all epiphyte groups. This proportion represents the probability of a bird perching on a branch supporting a given epiphyte group. Cylinders were set 1–2 m off trail at 20 m intervals totaling 211 cylinders. Non-vascular epiphytes (mosses and liverworts) were not considered because of the difficulty of seeing them from the ground, especially when they occur amidst vascular epiphytes. Likewise woody hemi-epiphytes (mainly *Ficus* spp., *Clusia criuva* and *Coussapoa microcarpa*) were not considered because they are ecologically and functionally similar to trees in regards to plant structure and the resources offered to birds. Bird selectivity was assessed for those species for which we had five or more records on epiphytes by the difference between the proportional foraging use (frequency) of a given epiphyte group by a bird species and the relative availability of that group (Sillett 1994). Based on the availability of epiphytes, 95% confidence intervals of the relative availability for each epiphyte group were calculated. If the difference between the frequencies of use of a given epiphyte group by a bird species was positive and higher than the epiphyte confidence interval, the bird species was considered selective for that particular epiphyte group. On the contrary, if the difference between the frequency of use of an epiphyte group was negative and less than the confidence interval, the bird species was considered non selective for the epiphyte group.

Statistical tests were implemented in the BioStat 2.0 package (Ayres *et al.* 2000).

RESULTS

We made a total of 74 records involving 24 bird species (12 families) that exploited epiphytes mainly in the understory (mean height ± SD = 4.6 ± 3.0 m, range 1–18 m, N = 74; Table 1). Most (70.8%) of the birds recorded were exclusively or predominantly insectivorous, although nectarivorous and frugivorous species were also recorded (Table 1). Thamnophilidae (four species), Trochilidae, Thraupidae and Furnariidae (three species each) were the most representative bird families (Table 1). Only three records from three bird species exploiting bromeliads did not involve foraging behavior [Green-headed Tanager (*Tangara seledon*) captured live leaf fibers as nest material, Flame-crested Tanager (*Tachyphonus cristatus*) and Yellow-legged Thrush (*Platycichla flavipes*) exploited tank bromeliads for bathing and drink water, respectively], totaling then 71 foraging records. Furnariidae (N = 25) followed by Dendrocolaptidae (N = 11) were the families most frequently recorded foraging on epiphytes. White-throated Woodcreepers (*Xiphocolaptes albicollis*), White-eyed Foliage-gleaners (*Automolus leucophthalmus*), and Black-capped Foliage-gleaners (*Philydor atricapillus*) were regular users, while the remainder species foraged in epiphytes only occasionally, being classified as

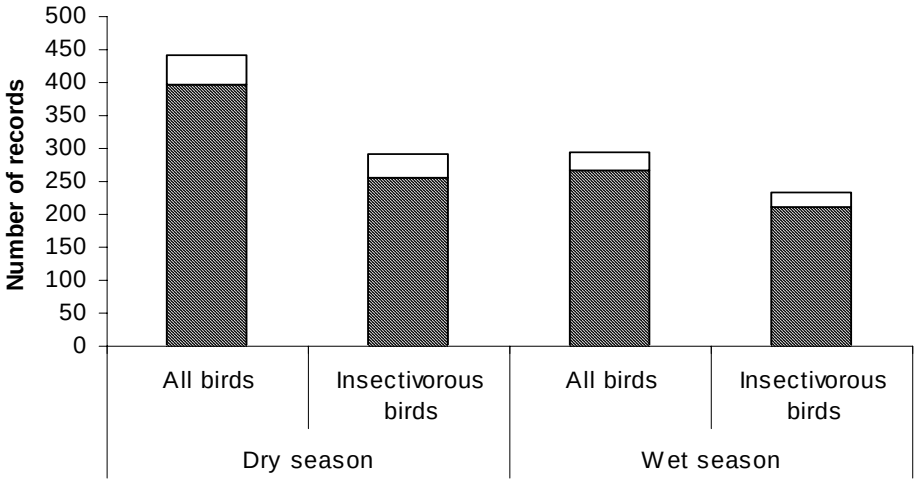

FIG 1. Number of records of all birds (nectarivorous, insectivorous and frugivorous) and insectivorous birds only exploiting non-epiphyte (hatched) and epiphyte (white) substrates in the dry (May to September 2005) and wet seasons (October to April 2005).

occasional users. No bird was classified as frequent user of epiphytes (Table 1).

All the surveyed epiphyte groups but Cactaceae were exploited by birds. Bromeliads followed by Araceae were the most frequent epiphytes (Table 1). Bromeliads were also responsible for the greater variety of resources exploited by birds, including arthropods, nectar, water for drinking and bathing, and nest material. Nectar was the most frequently exploited resource in bromeliads. In aroids (Araceae), three species of birds were recorded eating invertebrates and fruit. Pteridophyta, Gesneriaceae and Orchidaceae were visited only once by three distinct bird species (Table 1).

In addition to the bird species recorded foraging on epiphytes, we made an additional set of 663 foraging records in non-epiphyte substrates. Branches and live leaves of non-epiphytes were the most frequently used substrates (438 and 76 records, respectively), followed by trunks (69 records). No seasonal differences were detected either in the proportional use of epiphyte and non-epiphyte substrates by all birds ($G = 0.06$, $df = 1$, $P = 0.80$) or by insectivorous birds only ($G = 0.65$, $df = 1$, $P = 0.42$; Fig. 1). Similarly, the number of species exploiting epiphyte (dry season = 13 species; wet season = 18 species) and non-epiphyte substrates (dry season = 22 species; wet season = 21 species) did not differ seasonally ($G = 0.30$; $df = 1$; $P = 0.58$).

The relative availability of Bromeliaceae, Araceae, Pteridophyta, Gesneriaceae, Orchidaceae and Cactaceae were 38.3%, 29.7%, 12.9%, 10.3%, 6.6% and 2.0%, respectively. None of the bird species for which we had sufficient records were considered selective to any of the epiphyte groups (Table 1).

Furnariidae and Dendrocolaptidae had the greatest number of records of foraging on epiphytes while engaged in mixed-species flocks (Furnariidae, N = 23 and Dendrocolaptidae, N = 6). However, the presence in mixed-species flocks was significantly associated with the exploitation of epiphytes (Fis-

cher exact test: $P = 0.020$) only for the White-eyed Foliage-gleaner.

DISCUSSION

During 360 h of field observations we had 0.2 records/h of epiphyte exploitation, a figure substantially lower than the 2.1 records/h obtained by Nadkarni & Matelson (1989) during 289 h of observations in two consecutive months at Monteverde, a montane rainforest in Costa Rica. Unfortunately, the lack of studies in other Atlantic forest sites precludes similar comparisons. Possible explanations for the difference in the frequency of epiphyte use between Monteverde and JIES are threefold: first, as other Neotropical mid-elevation montane forests, Monteverde is home to the greatest taxonomic and structural diversity of epiphytes of any forest type (Madison 1977, Nadkarni & Wheelwright 2000), thus offering more opportunities for epiphyte use. Second, Nadkarni & Matelson (1989) studied bird utilization of both vascular and non-vascular (mosses, lichens) epiphytic substrates, the latter was not considered in our study. Third, they combined observations from the ground level and from platforms installed in the forest canopy, which permit the recording of interactions occurring in the upper canopy. Because of the dense vegetation covering our trails, we likely missed some of the interactions occurring in the highest trees (> 20 m). This might explain the relative lower average height of records we obtained (4.6 ± 3.0 m) in comparison with Pizo (1994 and unpubl.; 14.1 ± 5.2 m, N = 50), who made his observations in a more opened Atlantic forest site.

We recorded 24 bird species exploiting epiphytes, which represents 23% of the 104 species we recorded during the study. Considering community-wide studies of epiphyte utilization by birds (Nadkarni & Matelson 1989, Pizo 1994), and studies that reported foraging observations of Thraupidae, Furnariidae, and specially Trochilidae species in the Brazilian Atlantic forest (Rodrigues 1995, Sazima *et al.* 1995, Buzato *et al.* 2000, Mallet-Rodrigues 2001), we added 14 more species to the published list of birds that exploit epiphytes. In accordance with the general impression derived from the review of Nadkarni & Matelson (1989), a diverse assemblage of birds exploited epiphytes at JIES, including insectivorous, nectarivorous and frugivorous birds from the canopy and understory strata, most of them exploiting epiphytes only occasionally. Altogether these data reinforce the notion that the exploitation of epiphytes is essentially opportunistic for most species.

Bromeliaceae and Araceae were the epiphyte groups most exploited by birds, likely due to their high abundance at the study site. In another Atlantic forest site, Bromeliaceae comprised the bulk of interactions with birds (67%, N = 74; Pizo 1994). In comparison with aroids, bromeliads offer a greater variety of resources to birds. The morphology and arrangement of their leaves contribute to the presence of invertebrates and water accumulation (Nadkarni & Matelson 1989, Yanoviak *et al.* 2007), likely promoting its frequent use by birds.

Contrary to the expectation by Nadkarni & Matelson's (1989) that epiphytes can supply resources in periods of food scarcity, no seasonal difference in the proportional use of epiphytes for foraging was noted for JIES birds in general, and insectivorous birds in particular. The dry season is a period of general food shortage in the Atlantic forest, especially arthropods (Davies 1945, Develey & Peres 2000), and one could expect epiphytes providing a valuable source of food during this period. However, the availability of epiphyte arthropods may also decrease during the dry season, as Yanoviak *et al.* (2007) noted in Monteverde. Studies comparing the seasonal availability of nectar and fruits in epiphyte and non-epiphyte plants are lacking but

would be valuable to assess the role of epiphytes in providing food for birds in periods of general food scarcity.

Notwithstanding the opportunistic nature of epiphyte exploitation, a few species at each bird community studied to date exhibit a closer relationship with epiphytes. Around 7–8% of the bird species in Costa Rican montane forests (Nadkarni & Matelson 1989, Sillet 1994), and in a Bolivian Andean forest (Remsen 1985) were considered epiphyte specialists. At the Atlantic forest, *Cichlocolaptes leucophrys* is a good candidate as an epiphyte specialist. Although the low number of records for this species at JIES precludes any definite conclusion, its frequent exploitation of epiphytes has been noticed (Sick 1997, del Hoyo *et al.* 2003, Sigrist 2006).

We hypothesized that the participation in mixed-species flocks could favor the foraging in epiphytes because the putative protection against predators provided by mixed-flocks would facilitate the careful and time-consuming inspection required to capture arthropods amidst the leaves and roots of epiphytes. Although a great number of records of epiphyte exploitation involved three regular members of understory mixed-flocks, the White-eyed Foliage-gleaner, the Straight-billed Woodcreeper (*Xiphorhynchus fuscus*) and the Black-capped Foliage-gleaner (Develey & Peres 2000), only the White-eyed Foliage-gleaner exploited epiphytes more frequently when associated with mixed-species flocks than expected by chance. Future studies should carefully investigate the relationship between the participation in mixed-species flocks and epiphyte exploitation, especially for members of canopy flocks, which were poorly represented in our sample.

In summary, the use of epiphytes was opportunistic for most of the bird species recorded and occurred throughout the year at JIES. Bromeliaceae and Araceae were the plant families most frequently exploited, while Furnariidae and Dendrocolaptidae were the bird families that most frequently exploited epiphytes. Given the abundance and ecological importance of epiphytes in the Atlantic forest, there are ample opportunities for future studies, not only to add more epiphyte-exploiting bird species to the already known list, but also to fine-tune our understanding of interactions between epiphytes and birds. For instance, the likely specialization of some bird species (e.g., *Cichlocolaptes leucophrys*) on epiphytes remains to be quantitatively assessed as well as the role of birds as seed dispersers of fleshy-fruited epiphytes, a theme unexplored in the literature.

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