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Leaf Surface Specializations of Birds and *Arthropods* in a Panamanian Forest

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Summary. Most species of Panamanian lowland forest birds specialize on leaf undersurfaces when hunting foliage insects. The few species of leaf surface generalists and leaf upper surface specialists are omnivorous gleaners. We estimate that while over 90% of the avian understory insectivory is directed towards leaf undersurfaces, only 50% of canopy foliage insectivory is directed towards the undersides of leaves. In the low understory we found 70–80% of the arthropods on leaf undersides. The excess use of leaf-bottoms by understory birds may be a result of their greater visibility. It is hypothesized that less proficient insectivores are unable to take advantage of the greater effective density of underleaf insects because they can only efficiently attack the closest leaf surfaces; these closest surfaces will usually be the leaf tops from the branch on which the bird is perched. Alternatively, leaf-top specialists may have special foraging adaptations for overcoming the disadvantages of leaf-top foraging. These adaptations may involve attack behavior (*Tachyphonus luctuosus*) or searching behavior (*Dacnis cayana*). *Dacnis* often used leaf damage as a foraging cue; this may be the first report of a bird using leaf damage for searching for insects. The greater use of leaf upper surfaces by canopy birds may be influenced by four factors: greater seasonality of insects in the canopy favoring omnivores which may be less efficient insectivores; more insects on leaf tops; fewer planar leaf arrangements in canopy plants; or the greater visibility of leaf upper surfaces of the outer shell of foliage of massive trees. Based on the greater number of arthropods on leaf bottoms in the dry season, the higher abundance of smaller insects on leaf bottoms, as well as the greater proportion of insects on leaf tops at cooler higher elevations, we suggest that arthropods prefer leaf bottoms in tropical areas for physiological, not predator avoidance reasons.

tion from other species, and the efficiency with which the species can locate and attack prey on that surface. The relative importance of these factors, however, is usually unknown. Under most circumstances, comparing different substrates for prey availability or for the ease with which prey may be captured is complicated by the extreme qualitative differences between the surface types (but see Jackson, 1979). Simply sampling insects in an equivalent fashion, when comparing air, bark and foliage, is a difficult obstacle.

In this paper we present a preliminary analysis of foraging specialization on two substrates, the lower (LS) and upper (US) surfaces of broad leaves of tropical forest shrubs and trees. Some of the problems associated with comparing different surfaces are minimized, since the two surfaces have the same spatial distribution, and similar size, form, and texture.

Several distinct scenarios are possible for the use of the two leaf surfaces by a community of birds:

1. Both sides of the leaf might be equivalent in insect availability and require no specialization for hunting. In this case, presumably no surface specialization should be observed in foliage-gleaning birds.
2. Both sides might be equally rewarding, but require different hunting techniques. Under these conditions, leaf surfaces may be critical in resource partitioning to minimize competition.
3. One side might be significantly more rewarding and attract the attention of most foliage-gleaning birds. If insects on both sides are equally easy to attack, or if the richer side is more easily attacked, then all species should concentrate on the rich surface. But, if the more rewarding side is also more difficult to reach, only those species with the minimum proficiency to exploit the more difficult, albeit richer leaf surface should show specialization on that surface. Less specialized insectivores may be restricted to the poorer surface.

Introduction

The surface from which insects are captured has been a prominent variable in foraging studies of forest birds. Many studies group species into guilds or ecological roles on the basis of dominant foraging substrate (e.g., foliage-gleaning, bark-gleaning, etc.; Root, 1967; Cody, 1974; Karr, 1976a). Detailed studies of foraging behavior of species rely heavily on the prey-capture surface (Root, 1967; Williamson, 1971). While it is evident to any field observer that bird species do not forage off all possible surfaces, factors contributing to specialization are usually obscure. Presumably, the quality of a particular substrate for a species is effected by the relative availability of prey on the surface, potential competi-

Study Area

Birds were observed in the moist lowland forests of Barro Colorado Island (BCI, 9°09'N, 79°51'W) and the nearby Pipeline Road area in central Panama. A description of these areas can be found in Croat (1978) and Karr (1971). Both of these areas receive about 2,500 mm of rain falling mainly in a rainy season lasting from mid- or late April to mid-December. Most of the observations were made in the young (70–100 year old) and old (150+ year old) forests on BCI. Several species of foliage-gleaning birds characteristic of lowland Panamanian forests are not found on BCI (Willis and Eisenmann, 1979); expeditions (15 trips; 105 field h)

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were taken to the Rio Frijoles, Rio Limbo, Rio Mendoza and the Rio Agua Salud in the Pipeline Road forest. These areas have forest that is some late stage of second growth. All insect sampling was conducted in young forest on the plateau or Lutz Ravine of BCI.

Methods

Bird Foraging

Observations were made on birds on designated transects. So far as possible, we observed foraging of only one or two species on a given walk. Some of the canopy species were observed from a 40 m tower or from the edge of the BCI laboratory clearing. We recorded the surface for up to 5 foraging maneuvers (including twig, branch, trunk, palm frond, ground, air, flower, fruit, dead leaf, US, and LS), defined as those after which prey was seen to be eaten or bill-wiping observed. Successful foraging is nearly always followed by bill-wiping in most species. Sample sizes for many species were small because they are rare, or difficult to observe and foraging rates are often low.

Relative Use of Surfaces

The relative amount of foraging on the two surfaces can be approximated by combining foraging and census data in a manner similar to that of Emlen (1978). The relative abundance of each species is multiplied by the estimated existence energy per individual (formulae and weights from Karr, 1971 or own data). This product is multiplied by the portion of foraging directed to the two leaf surfaces. The weighted consuming biomass is summed over all species for each surface and the overall proportion is calculated. The major assumption in this calculation is that birds capture the same size arthropods from the two surfaces.

Every census technique for tropical forest birds is biased to a different subset of the avifauna (Karr, 1976a). We have analyzed three different sets of census data to help circumvent this bias: a transect census on BCI, a spot census from canopy tower on BCI (Greenberg, MS), and density estimates of understory birds based on mist-netting (Karr, 1971).

The transect, traversing both young and old forest on BCI, was 1 km long by 30 m wide; we slowly paced the trail section for 150 min between 0645–1000h on 22 occasions from October 1978 to May 1979. This census technique is probably biased against high canopy or shy low understory species.

Canopy censuses were conducted from a 40 m tower in young forest. All birds in the outer canopy of a 2.7 ha area around the tower were counted. The censuses were conducted for two hours at dawn or dusk. The results used here are based on 40 censuses between November 1978 and May 1979.

For the Pipeline Road mist-netting data, we used density estimates determined by Karr (1971) for all species that he designated as Low or Medium Strata. Beyond the obvious bias of this data set to understory species, mist-netting probably over-estimates mobile species with overlapping home-ranges, such as manakins (Karr, 1976a). These results exclude migrants which are well represented in the BCI census data. Migrants are apparently scarce in the understory of the Limbo Hunt Club area, where the study was conducted (Karr, 1976c).

Insect Distribution

We conducted 9 censuses between November 1978 and September 1979 to record the abundance of arthropods on the two leaf surfaces in the low understory. The censuses consisted of direct examination of 11,000 leaves along transects through the young forest on the BCI plateau. All leaves within arms length (maximum of 100 leaves per plant) of the transect were examined after slowly approaching the shrub or tree to watch for escaping insects. Probably only a few fast-flying dipterans or hymenopterans were missed on the census because they flushed. Foliage was examined 1–5 m from the ground with the aid of a 3.2 m step ladder. Each census consisted of 4,000 leaves in low (1–2 m) open understory, 4,000 leaves in low dense vine-tangles by old tree falls, and 3,000 leaves in high (2–5 m) open understory. Censuses were conducted in mid-day (1,000–1,500) over several days each month (except December) and twice in May. A total of 99,000 leaves or leaflets were examined. Insects were identified to gross taxonomic categories (orders and some families) and classified by dominant color and size.

Canopy insects were censused by climbing to a height of 25–35 m on the BCI canopy tower and examining leaf surfaces closest to the trees with binoculars. Leaf surfaces were censused on *Anacardium excelsum* (Bertero and Balb) Skeels Anacardiaceae (2 individuals), *Virola surinamensis* (Rol.) Warb. Myrtaceae (2), *Ficus yoponensis* Dejv. Moraceae (1), and the vine *Uncarea tomentosa* (Willd.) D. C. Rubiaceae. Six censuses were conducted in mid-wet season (July–August); 3 during the early morning peak of bird activity in the canopy (600–800 h), and 3 in the late morning 1000–1200 h. Since individual leaves were not censused, only visible surfaces, different number of LS and US were censused and the results were standardized to insects/1,000 surfaces. This sample is biased towards leaf surfaces visible from the tower and represents only a few species of plant; how these biases might affect the results is unknown.

Ecological Classification of Foliage-Gleaning Birds

At least 45 species hunt foliage insects in the BCI forest. An additional 12 species of foliage-gleaners occur in the Pipeline Road forest (Table 1). These species are classified by dominant foraging tactic and commitment to insectivory for further analysis.

Foraging tactic: We discerned two major classes of foraging behavior, corresponding to the hoverers and gleaners of Orians (1969) and the snatchers and gleaners of Pearson (1975). The gleaners (27 spp.) search actively and continuously usually attacking insects by picking them off at short range. The second group, hoverers (28 spp.), may remain motionless for long periods and usually attack insects from greater distances by rapidly leaping at leaves. True hover-gleaning, where birds remain motionless in flight by a leaf, is relatively rare in Panamanian forest birds. While in most cases the dichotomy between hoverer and gleaner is clear, a few intermediates occur; these are either very sluggish gleaners (*Hylophilus ocharceiceps* and *Thamnophilus punctatus*) or mobile hoverers (*Dysithamnus puncticeps*). One additional, yet minor group of foliage foragers is the terrestrial leapers, which includes *Oporornis formosus* and *Myrmeciza exsul*; these species leap up from the ground to glean low understory foliage.

Commitment to insectivory: We have divided the species based on commitment to insectivory throughout the year: a) committed insectivores (CI), including antbirds and some tyrannids, appear to be restricted to insectivory; b) partially-committed insectivores

Table 1. Categorization of leaf surface preference and other ecological information about foliage-gleaning birds in lowland forests of Central Panama

Species	Hunting Method	Location	Commitment to Insectivory	Surface Preference	Source
<i>Thalaurania colombica</i>	Glean	BCI ^a	0	LS	Angher pers. comm.
<i>Damophila julie</i>	Glean	BCI	0	LS	Angher pers. comm.
<i>Trogon rufus</i>	Hover	BCI	0	LS	This study
<i>Malacoptila panamensis</i>	Hover	BCI	CI	?	
<i>Thamnophilus punctatus</i>	Glean	BCI	CI	LS	This study
<i>Thamnistes anabatinus</i>	Glean	Pipeline	CI	?	
<i>Dysithamnus puncticeps</i>	Hover	BCI	CI	LS	This study
<i>Myrmotherula brachyura</i>	Glean	Pipeline	CI	?	
<i>Myrmotherula axillaris</i>	Glean	BCI	CI	LS	This study
<i>Microrhopias quixensis</i>	Glean	BCI	CI	LS	This study
<i>Myrmeciza exsul</i>	Leap	BCI	CI	LS	Willis and Oniki, 1972
<i>Pipra coronata</i>	Hover	Pipeline	0	LS	This study
<i>Pipra mentalis</i>	Hover	BCI	0	LS	Worthington pers. comm.
<i>Schiffornis turdinus</i>	Hover	Pipeline	PC	LS?	Skutch, 1969
<i>Sapayoa aenigma</i>	Hover	Pipeline	PC	LS	This study
<i>Laniocera rufescens</i>	Hover	BCI	?	LS? ^b	
<i>Rhytipterna holerythra</i>	Hover	BCI	PC?	LS	This study
<i>Lipaugus unirufus</i>	Hover	BCI	PC?	LS? ^b	
<i>Tityra sp.</i>	Hover	BCI	0	LS? ^b	
<i>Querula purpurata</i>	Hover	BCI	0	LS	This study; Snow, 1971
<i>Myiarchus tuberculifer</i>	Hover	BCI	PC	G	This study
<i>Empidonax virescens</i>	Hover	BCI	PC	LS	This study
<i>Myiobius sulphureipygius</i>	Hover	Pipeline	CI	LS	This study
<i>Terenotriccus erythrurus</i>	Hover	BCI	CI	LS	This study
<i>Platyrinchus coronatus</i>	Hover	BCI	CI	LS	This study
<i>Cnipodectes subbrunneus</i>	Hover	Pipeline	PC	LS	This study
<i>Tolmomyias assimilis</i>	Hover	BCI	PC	LS	This study
<i>Rhynchocyclus olivaceus</i>	Hover	BCI	CI	LS	This study
<i>Oncostoma olivaceum</i>	Hover	BCI	CI	LS	This study
<i>Myiornis atricapillus</i>	Hover	BCI	CI	LS	This study
<i>Phylloscartes flavovirens</i>	Hover	Pipeline	PC?	LS? ^b	
<i>Myiopagis gaimardii</i>	Hover	BCI	CI	LS	This study
<i>Tyranniscus vilissimus</i>	Hover	BCI	0?	LS	This study
<i>Ornithion brunneicapillum</i>	Hover	BCI	PC	LS? ^b	
<i>Mionectes olivaceus</i>	Hover	Pipeline	0	LS?	
<i>Pipromorpha oleaginea</i>	Hover	BCI	0	LS	This study
<i>Polioptila plumbea</i>	Glean	BCI	CI	LS?	This study
<i>Smaragdolanus pulchellus</i>	Glean	BCI	CI	?	
<i>Vireo flavifrons</i> M	Glean	BCI	PC	?	
<i>Vireo olivaceus</i> M	Glean	BCI	0	?	
<i>Hylophilus decurtatus</i>	Glean	BCI	PC	LS	This study
<i>Hylophilus ochraceiceps</i>	Glean	Pipeline	CI	LS	This study
<i>Coereba flaveola</i>	Glean	BCI	0	?	
<i>Cyanerpes lucidus</i>	Glean	BCI	0	?	
<i>Cyanerpes cyaneus</i>	Glean	BCI	0	US	Snow and Snow, 1971
<i>Dacnis cayana</i>	Glean	BCI	0	US	This study
<i>Vermivora peregrina</i> M	Glean	BCI	0	?	
<i>Dendroica castanea</i> M	Glean	BCI	0	G	This study
<i>Dendroica pensylvanica</i> M	Glean	BCI	PC	LS	This study
<i>Wilsonia canadensis</i> M	Glean	BCI	CI	LS	This study
<i>Geothlypis formosus</i> M	Leap	BCI	CI	LS	Willis, 1966
<i>Cacicus uropygialis</i>	Glean	BCI	PC	G?	This study
<i>Piranga rubra</i>	Glean	BCI	0	?	
<i>Chlorothraupis carmioli</i>	Glean	Pipeline	0	G	This study
<i>Tachyphonus luctuosus</i>	Glean	BCI	0	US	This study
<i>Heterospingus rubrifrons</i>	Glean	BCI	0	US	This study
<i>Mitrospingus cassinii</i>	Glean	Pipeline	0	G?	This study

^a BCI refers to species found on BCI; Pipeline refers to species found only on Pipeline road

^b For the overall tally, these species are assumed to be LS foragers since they are hoverers

^c M = Migrant

(PCI) are primarily insectivorous but occasionally switch to other foods, particularly during periods of high fruit and flower abundance; and c) omnivores (0) commonly take fruit or nectar either throughout the year (e.g., Trogons, manakins) or seasonally (e.g., tanagers).

Results

Leaf Surface Preference in Relation to Foraging Tactic and Commitment to Insectivory

Forty-one species are probably LS specialists, 4 species are probably US specialists, and 5 species are probably generalists (Table 1). Species for which we collected foraging data are discussed below by foraging behavior class.

Hoverers. Hoverers nearly always take insects off LS; we observed 359 foraging motions to LS and 18 to US (Table 2). The quick upward movement probably precludes common US foraging. A partial exception was the *Myiarchus tuberculifer*; this species is a true hover-gleaner and flew up or down before hovering at a leaf.

Gleaners. More variation in leaf surface preference exists within the gleaners. To further examine patterns of leaf surface preference, we gathered observations from species in each class of commitment to insectivory: 5 species of CI, 2 species of PCI, and 5 species of 0 (Table 3). Since the sample sizes of foraging observations for most of these species is on the order of 50–100, and have large expected confidence intervals, we will distinguish only 3 classes in terms of specialization on leaf surfaces: LS specialists (70% or more foraging off LS); generalists (31–69% foraging off LS); and US specialists (70% or more off US).

All species except those in the 0 class are specialized LS foragers. The understory-dwelling *Chlorothraupis carmioli*, canopy-dwelling *Dacnis cayana* and migrant *Dendroica castanea* were leaf surface generalists. The two canopy tanagers, *Tachyphonus luctuosus* and *Heterospingus rubrifrons*, were US specialists. Three species that we initially assumed were foliage foragers were only observed to hunt off foliage occasionally. The small sample sizes intimate that all three species were leaf surface generalists.

Foraging Pressure on the Two Leaf Surfaces

While a majority of species specialize on LS, because of the rarity of many tropical forest birds a greater overall use of LS cannot be inferred. A rough idea of the relative use can be generated by the estimation procedure outlined in Methods. The complete analysis is presented in Tables 4–6. LS foraging appears to be highest for the Pipeline Road understory species (92%). The transect data, biased towards mid-level birds, also produced a substantial dominance for LS foraging (75%). The canopy birds showed the least overall use of LS (51%). This probably results from the high abundance of *Tachyphonus luctuosus*, *Dacnis cayana*, and *Dendroica castanea*.

Distribution of Arthropods

Most arthropods were found on LS of understory plants (79% $n=1234$; Table 7). It is, however, unlikely that all arthropods are equally attractive to avian predators: most adult dipterans are probably too fast for birds to catch; brightly colored insects

Table 2. Leaf surface preference and degree of foliage insectivory of 20 species of hoverer^a

Species	LS	US	Other ^b
<i>Trogon rufus</i>	7	0	3
<i>Dysithamnus puncticeps</i>	33	3	7
<i>Pipra coronata</i>	15	0	5
<i>Sapayoa aenigma</i>	18	0	3
<i>Rhytipterna holerythra</i>	6	1	3
<i>Tityra sp.</i>	3	0	? ^c
<i>Querula purpurata</i>	6	0	?
<i>Myiarchus tuberculifer</i>	14	10	5
<i>Empidonax virescens</i>	15	0	1
<i>Myiobius sulphureipygius</i>	24	0	11
<i>Terenotriccus erythrurus</i>	40	2	6
<i>Platyrinchus coronatus</i>	5	0	0
<i>Cnipodectes subbrunneus</i>	5	0	1
<i>Tolmomyias assimilis</i>	30	0	2
<i>Rhynchocyclus olivaceus</i>	17	0	3
<i>Oncostoma olivaceum</i>	47	1	3
<i>Myiornis atricapillus</i>	5	0	0
<i>Myiopagis gaimardii</i>	0	1	0
<i>Tyranniscus vilissimus</i>	7	0	3
<i>Pipromorpha oleaginea</i>	10	0	?
Total	359	18	69+

^a Figures are actual numbers of observations

^b Including frugivory which is counted once per individual observed

^c Species for which frugivorous observations were not recorded

Table 3. Leaf surface preferences of gleaners classified by commitment to foliage insectivory

	N	% Foliage ^b	% US ^c	% LS
Non-foliage gleaners ^a				
<i>Poliophtila plumbea</i>	46	15	29	71
<i>Cacicus uropygialis</i>	45	22	64	37
<i>Mitrospingus cassinii</i>	40	25	67	33
Committed Foliage-gleaner				
<i>Thamnophilus punctatus</i>	84	71	18	82
<i>Myrmotherula axillaris</i>	150	82	22	78
<i>Microrhopias quixensis</i>	181	94	15	85
<i>Hylophilus ochraceiceps</i>	40	88	3	97
<i>Wilsonia canadensis</i>	60	90	0	100
Partially-committed				
Foliage-gleaner				
<i>Dendroica pensylvanica</i>	353	90	14	86
<i>Hylophilus decurtatus</i>	106	88	17	83
Omnivores				
<i>Dendroica castanea</i>	576	55	43	57
<i>Dacnis cayana</i>	102	65	70	30
<i>Chlorothraupis carmioli</i>	59	63	35	65
<i>Tachyphonus luctuosus</i>	61	81	84	16
<i>Heterospingus rubrifrons</i>	24	50	100	0

^a Species that gleaned insects off foliage, as opposed to other substrates, less than 50%

^b Percent of all foraging observations; frugivory counted once per individual

^c Percent of foliage-foraging observations

Table 4. Relative foraging pressure estimated from relative abundances presented by Karr (1971)

Species	Relative Abundance (A)	Weight (W)	$A \times W^{2/3}$	US	LS
<i>Pipra mentalis</i>	0.24	15 g	1.40	0.02 ^b (0.03) ^c	0.25 (0.35)
<i>Pipra coronata</i>	0.12	10	0.55	0.02 (0.01)	0.50 (0.28)
<i>Myrmotherula axillaris</i>	0.09	8	0.36	0.18 (0.06)	0.64 (0.23)
<i>Terenotriccus erythrurus</i>	0.07	7	0.25	0.04 (0.01)	0.80 (0.20)
<i>Thamnophilus punctatus</i>	0.06	24	0.49	0.13 (0.06)	0.58 (0.28)
<i>Microhoppia quixensis</i>	0.06	8	0.24	0.14 (0.03)	0.80 (0.19)
<i>Platyrinchus coronatus</i>	0.06	9	0.26	0.02 (0.005)	0.90 (0.23)
<i>Pipromorpha oleaginea</i>	0.06	10	0.27	0.02 (0.005)	0.25 (0.07)
<i>Cnipodectes subbrunneus</i>	0.04	24	0.32	0.02 (0.005)	0.50 (0.16)
<i>Rhynchocyclus olivaceus</i>	0.04	22	0.31	0.02 (0.006)	0.85 (0.26)
<i>Myiobus sulphureipygias</i>	0.04	12	0.21	0 (0)	0.67 (0.14)
<i>Oncostoma olivaceum</i>	0.02	7	0.07	0.02 (0)	0.94 (0.07)
<i>Malacoptila panamensis</i>	0.02	44	0.20	?	?
<i>Shiffornis turdinus</i>	0.02	33	0.20	0.02 (0)	0.50 (0.10)
<i>Chlorothraupis carmioli</i>	0.02	34	0.20	0.22 (0.04)	0.44 (0.08)
<i>Sapayoa aenigma</i>	0.01	21	0.07	0.08 (0)	0.85 (0.06)
Sum of relative consuming biomass				0.245	2.700
Percentage of total foliage-gleaning consuming biomass				8	92

^a Hoverers with small sample sizes have mean values of LS versus US foraging substituted (for hoverers excluding *Myiarchus tuberculifer*)

^b Number is estimated proportion of foraging on US

^c Number is proportion of foraging $\times (A \times W^{2/3})$ or relative consuming biomass

Table 5. Relative foraging pressure based on transect counts conducted on Barro Colorado Island (see Table 4)

Species	Relative Abundance (A)	Weight (W)	$A \times W^{2/3}$	US	LS
<i>Dendroica castanea</i>	0.175	11 g	0.85	0.26 (0.20)	0.31 (0.26)
<i>Microhoppia quixensis</i>	0.130	8	0.51	0.14 (0.07)	0.80 (0.41)
<i>Hylophilus decurtatus</i>	0.093	9	0.40	0.15 (0.06)	0.73 (0.29)
<i>Thamnophilus punctatus</i>	0.078	24	0.76	0.13 (0.10)	0.58 (0.44)
<i>Myrmotherula axillaris</i>	0.058	8	0.23	0.18 (0.04)	0.64 (0.15)
<i>Tachyphonus luctuosus</i>	0.070	12	0.36	0.68 (0.24)	0.13 (0.05)
<i>Dendroica pensylvanica</i>	0.045	9	0.19	0.13 (0.02)	0.77 (0.15)
<i>Dysithamnus puncticeps</i>	0.043	18	0.29	0.03 (0.01)	0.80 (0.23)
<i>Tolmomyias assimilis</i>	0.035	13	0.19	0 (0)	0.92 (0.17)
<i>Vermivora peregrina</i>	0.025	9	0.11	?	?
<i>Myrmeciza exsul</i>	0.023	27	0.20	0.50 (0.10)	0 (0)
<i>Polioptila plumbea</i>	0.023	7	0.08	0.05 (0)	0.10 (0.008)
<i>Coereba flaveola</i>	0.023	7	0.08	?	?
<i>Dacnis cayana</i>	0.023	13	0.13	0.20 (0.03)	0.46 (0.06)
<i>Empidonax virescens</i>	0.018	15	0.10	0 (0)	0.85 (0.09)
<i>Querula purpurata</i>	0.018	?	?	?	?
<i>Ornithion bruneicapillum</i>	0.018	6	?	?	?
<i>Geothlypis formosus</i>	0.018	15	0.10	0.50 (0.05)	0 (0)
<i>Terenotriccus erythrurus</i>	0.015	7	0.05	0.04 (0)	0.80 (0.04)
<i>Myiarchus tuberculifer</i>	0.015	29	0.14	0.33 (0.04)	0.48 (0.07)
<i>Myiornis atricapillus</i>	0.013	6	0.04	0.05 (0)	0.90 (0.04)
<i>Oncostoma olivaceum</i>	0.013	7	0.05	0.02 (0)	0.94 (0.05)
<i>Pipra mentalis</i>	0.010	15	0.06	0.05 (0)	0.20 (0.01)
Sum of relative consuming biomass				0.960	2.518
Percentage of total foliage-gleaning consuming biomass				21.5	78.5

may be avoided; extremely keratinized or very small insects may also be ignored. After eliminating very small (< 2 mm) or brightly colored arthropods, isopods, and flies, there was still a dominance of LS arthropods (80% $n=922$). When in addition to the above

restrictions only arthropods greater than 5 mm were considered, the similar results were obtained (71% $n=223$). In fact, all orders except dipteran, and hymenoptera (Table 7) showed a bias towards occurring on LS. Within this dominance of LS insects, there

Table 6. Relative foraging pressure based on canopy census (see Table 4)

Species	Relative Abundance (A)	Weight (W)	$A \times W^{2/3}$	US	LS
<i>Dendroica castanea</i>	0.190	11 g	0.92	0.31 (0.29)	0.26 (0.24)
<i>Dacnis cayana</i>	0.118	13	0.56	0.46 (0.26)	0.20 (0.11)
<i>Hylophilus decurtatus</i>	0.103	9	0.44	0.15 (0.07)	0.73 (0.32)
<i>Cyanerpes cyaneus</i>	0.087	11	0.42	0.20? (0.08)	0 (0)
<i>Coereba flaveola</i>	0.071	7	0.26	?	?
<i>Tachyphonus luctuosus</i>	0.067	12	0.35	0.68 (0.24)	0.13 (0.05)
<i>Vermivora peregrina</i>	0.051	9	0.22	?	?
<i>Myiarchus tuberculifer</i>	0.035	29	0.32	0.33 (0.11)	0.48 (0.16)
<i>Tyranniscus vilissimus</i>	0.035	6	0.11	0.03? (0.003)	0.47 (0.05)
<i>Poliophtila plumbea</i>	0.035	7	0.13	0.04 (—)	0.10 (0.01)
<i>Cyanerpes lucidus</i>	0.030	?	?	?	?
<i>Piaya cayana</i>	0.030	?	?	?	?
<i>Thamnophilus punctatus</i>	0.026	24	0.21	0.43 (0.12)	0.58 (0.12)
<i>Piranga rubra</i>	0.026	29	0.28	?	?
<i>Microhospas quixensis</i>	0.020	8	0.089	0.14 (0.01)	0.80 (0.06)
<i>Tolmomyias assimilis</i>	0.020	13	0.110	0 (0)	0.92 (0.10)
<i>Dacnis venustus</i>	0.020	15	0.12	?	?
<i>Dendroica pensylvanica</i>	0.015	9	0.06	0.13 (—)	0.77 (0.05)
<i>Ornithion brunneicapillum</i>	0.015	6	0.05	?	?
Sum of relative consuming biomass				1.183	1.27
Percentage of total foliage-gleaning consuming biomass				48%	52%

Table 7. Numbers of arthropods found on upper and lower leaf surfaces on understory censuses categorized by major taxa and census period

Arthropod taxa	Nov.	Jan.	Feb.	Mar.	Apr.	May I ^c	May II	July	Aug.	Total
Araneida	22 ^a :4	21:2	44:2	57:1	50:1	37:1	17:1	27:1	69:3	334:16
Opilionidae	0:0	0:2	1:8	0:0	1:2	2:1	0:1	0:6	0:1	4:21
Coleoptera	22:10	21:4	37:0	50:1	29:7	18:4	33:6	26:15	19:22	255:49
Orthoptera	8:3	10:2	9:1	8:1	6:1	3:10	5:3	4:5	6:0	59:26
Lepidoptera (larvae)	1:3	0:0	0:0	0:2	3:0	0:0	78 ^b :3	8:2	1:0	21:10
Lepidoptera (adult)	1:7	0:0	6:5	5:0	4:0	3:0	5:4	7:0	6:3	37:19
Homoptera	4:3	11:3	15:1	14:1	12:3	9:3	19 ^b :5	27:0	22:7	133:26
Hemiptera	0:0	1:0	0:0	13:1	0:1	5:4	0:7	14:11	2:2	35:26
Diptera	2:16	1:7	3:3	5:1	7:1	7:6	0:5	5:6	7:4	37:49
Hymenoptera (no ants)	0:1	1:1	0:2	0:2	4:1	3:2	1:0	0:3	0:0	9:12
Neuroptera	3:0	1:0	2:0	0:0	0:0	1:0	0:0	1:0	2:0	10:0
Isopoda	3:1	0:0	1:0	0:0	0:0	0:0	0:0	1:0	0:0	5:1
Phasmidae	0:0	1:0	3:0	0:0	1:0	1:1	0:0	0:0	0:0	6:1
Other groups	3:1	1:0	1:0	0:1	2:0	2:2	2:0	1:1	6:1	18:6
Totals	69:49	69:21	122:22	152:11	119:17	91:34	81:35	121:50	140:23	963:264

^a Lower surface: upper surface arthropods

^b Found in a few large clusters. Only counted as one individual on census totals

^c May I is early and May II late May

was some seasonality; more arthropods were found on LS during dry season samples ($\bar{X}=0.86 \pm 0.035$ S.E. January–April) than wet season samples (0.73 ± 0.05 November, May–August, $U=17$ $p < 0.01$).

Within insect groups, larger insects are less restricted to LS. In coleoptera 12% of those less than 2 mm ($n=119$) and 21% of those greater than 2 mm (185) were found on LS ($\chi^2=4.7$, d.f.=1, $p < 0.05$). For orthopterans, 12% of those less than 6 mm ($n=25$) and 40% of those greater than 6 mm ($n=52$) were found on US ($\chi^2=6.4$, d.f.=1, $p < 0.01$). In homoptera 15% of those less than 6 mm ($n=108$) and 48% of those greater than 6 mm ($n=21$) were on US ($\chi^2=11.7$, d.f.=1, $p < 0.01$).

The difficulty of censusing canopy insects prevented a complete census, but some data were obtained to indicate trends in distribution. Table 8 presents the number of arthropods per thousand leaves (excluding hymenoptera, diptera and all arthropods less than 2 mm) for US and LS of 4 species of canopy plant. After standardization to arthropods per thousand surfaces, 58% of all arthropods were found on LS. If an overall average of species values is computed, to equalize for different number of surfaces checked per species, then 63% of all arthropods were found on LS. These data suggest that arthropods are more common on LS in the canopy.

Table 8. Number of arthropods found on leaf upper and lower surfaces during canopy insect censuses (see text)

Plant Species	Upper Surface			Lower Surface		
	Number of Surfaces	Number of Arthropods	Arthropods 1,000 surfaces	Number of Surfaces	Number of Arthropods	Arthropods 1,000 surfaces
<i>Anacardium excelsum</i>	2,214	11	5	1,744	15	9
<i>Virola surinamensis</i>	1,872	4	2	1,081	11	10
<i>Ficus yoponensis</i>	3,736	15	4	3,708	14	4
<i>Uncarea tomentosa</i>	2,693	6	2	1,846	4	2
Total	10,515	36	3.5	8,469	44	5
Percent of total		42	37		58	63

Discussion

The higher density of arthropods may be sufficient to explain the greater use of LS by birds. Arthropods were approximately four times more common on LS than US in the understory. The relative use of LS by understory birds, however, was probably substantially greater than these ratios. For the Pipeline Road estimates, nine times more foraging was done off LS than US. The 80% value for proportion of arthropods on LS is significantly different from an expected value of 91% based on the foraging data ($\chi^2=24.2$, $p<0.001$). Similar values would be obtained if all canopy birds were eliminated from transect data from BCI.

The 80% value is high since larger arthropods were less commonly found on LS (71%). The large biomass represented by these larger size class doubtlessly bias the total biomass towards the lower value.

Visibility of leaf surfaces is possibly important. A greater number of LS than US are probably visible and attackable for most foliage-gleaning birds. A bird is slightly elevated from the branch on which it is perched (Fig. 1); in the case of a small foliage-gleaner, such as a warbler or antwren, this distance is 3.5–5.0 cm. In most trees, leaves (or leaflets) are arranged on a horizontal plane to the branch (70% of all branches on study site, Greenberg in prep.). This arrangement provides the maximum projection on the horizontal plane below the bird and would tend to obscure visibility and discourage mobility downward (Fig. 1). In fact, the arc of obscured vision is potentially great, particularly for areas just below the bird and for branches with large leaves. The arc can be obtained for the vertical line of vision by the expression $2(\arccos e/L)$ where e is the vertical distance between the eye and branch and L is the horizontal component of the length of the leaf. For an antwren or warbler and a 15 cm leaf, the arc of obscured vision is 160°. This arc decreases as the line of vision of the bird crosses the branch ahead of the bird: $\text{arc} = 2(\arccos e^2 + b^2/L)$ where b is the distance from the bird that the line of vision crossed the branch. For example, at 25 cm ahead of the warbler the arc of obscured vision created by a 15 cm leaf is 120°.

Even if the petioles are angled or curved upward, the majority of obstructions will occur below and lateral to the bird. If the foliage is dessucate or spiralled some leaves will obscure vision to higher branches, but because of the elevated position of the bird eye over the branch, more foliage will be below the plane of the eye than above it. Any leaf arrangement should favor upward to downward vision and movement, although more plagio-

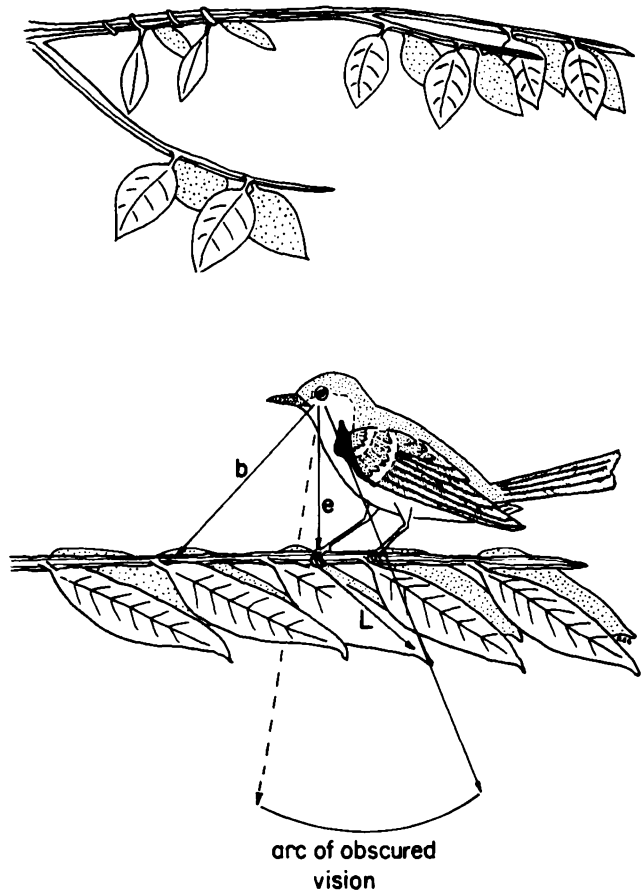


Fig. 1. Schematic diagram of *Dendroica pensylvanica* demonstrating the potential obstruction of vision. The arc of obscured vision is given by $2(\arccos e^2 + b^2/L)$ where L is leaf length, b is distance from bird's eye that the line of vision crosses the branch, and e is the height of the bird's eye above the branch

tropic arrangements will increase the effect. This effect will be negligible if leaf densities on the branch are low or if branch densities are so great that leaves from higher branches are commonly within 5 cm above the foraging bird. In most circumstances leaf densities are high and branch densities are low so the effect is potentially real.

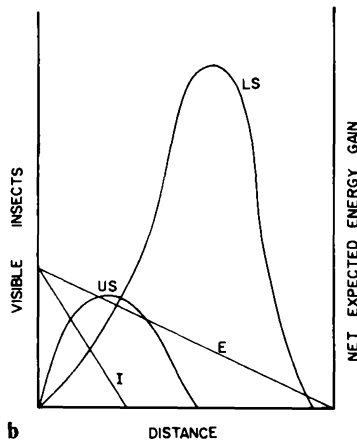
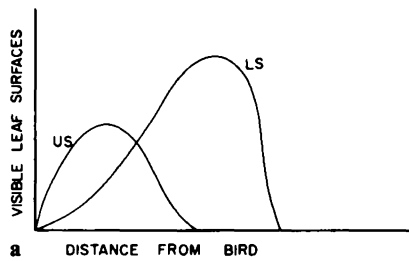


Fig. 2a and b. Model for the availability of visible insects at increasing distance from a bird. **a** Leaf surfaces visible as a function of distance (*LS*=lower surface and *US*=upper surface). **b** Relative number of insects visible at increasing distance given by weighting the *LS* curve by a constant factor (2) representing the greater abundance of insects on *LS*. Also graphed is the net expected energy curve for attacking an insect at increasing distance for Efficient (*E*) and Inefficient (*I*) insectivores

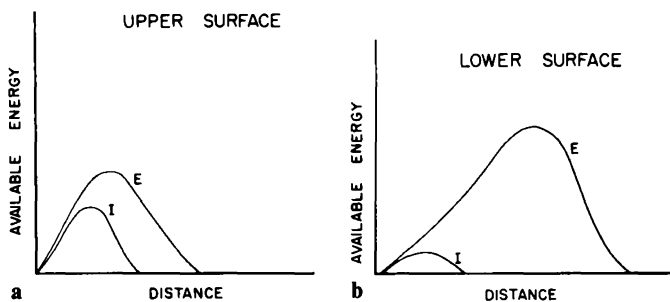


Fig. 3a and b. Expected energy gain from attacking all insects available at increasing distance for **a** US and **b** LS. Curves are the product of values on the insect availability curves and net expected energy gain curves in Fig. 2b

Leaf Foraging: a Model

Nearly all species of birds behaved as if the effective density of available arthropods was greater on *LS* than *US*. Under what circumstances should species forage off the more insect-poor *US*? Below we outline two possible circumstances: inefficient insectivory and specialization for *US* foraging.

Inefficient Insectivory. In areas of low to moderate branch density, the leaves closest to a foraging bird will be on the same branch

with their *US* towards the bird. At greater distances more *LS* should be visible (see previous section), but nearer the bird more *US* will be visible. An inefficient forager may be unable to detect or attack insects at a great distance and so be restricted to searching the closest leaves. This would bias available leaf surfaces in favor of *US*. This critical assumption, that birds will attack more *US* at a closer range is supported by foraging data from *Dendroica castanea*. Attack distances for *US* foraging averaged 10 cm (S.D. = 2.5 cm, $n = 79$) and for *LS* averaged 29 cm (S.D. = 4 cm, $n = 108$).

The following graphical model clarifies this argument. Fig. 2a presents the cumulative number of leaf surfaces visible to a foraging bird at increasing distances. The curve for *US* has higher values than the *LS* curve at closer range, but the *LS* curve surpasses the *US* curve farther away (see previous section). Both curves have a limit representing the point at which the visual field is totally obstructed or the limits of visual acuity. In Fig. 2b the *LS* curve has been multiplied by a constant (2) to reflect the greater number of insects per leaf; these curves represent insect availability at different distances. Two decreasing lines represent, for Efficient (*E*) and Inefficient (*I*) insectivores, the decreasing expected energy gain from attacking the same size insect at different distances. The line for the inefficient species decreases more rapidly because it cannot attack effectively at greater distances. Figures 3a and b present for the two species the energy availability curves for *US* and *LS* at different distances. These are obtained by taking the product of values on the availability and expected energy gain curves in Fig. 2. The energy availability curves present what a bird should gain by attacking all insects it sees, as a function of distance. For inefficient species the curves for *US* and *LS* are similar, with slightly higher values for *US*. For efficient species, the available energy for *LS* is far greater. Not surprisingly, the energy availability curves are smaller for the inefficient than the efficient species.

This model leads to the following predictions: 1) less efficient insectivores will forage more off *US*; 2) less efficient insectivores can expect far less gain from foliage insectivory and should switch to other food types more readily, if these food types are easily procured (e.g., some types of fruit); and 3) upper surface foragers or generalists are more likely to be omnivorous. The last prediction is consistent with data presented in this paper for gleaners (all *US* foragers or generalists were omnivores) and can be independently tested in other tropical forest communities.

Hoverers with long attack distances, such as manakins or *Pipromorpha*, are often omnivorous or frugivorous. This might contradict the predictions of this model were it not for a dichotomy that exists in the fruits that birds eat. Some fruits require the highly specialized attack behaviors of hovering and leaping, whereas other fruits are easily obtained by any foraging tactic. This latter type of fruit (such as *Miconia argentea* Melastomaceae) is what omnivorous gleaners usually forage on. The attack behavior required for difficult to exploit fruit and *LS* are the same; other factors, such as bill morphology or searching behavior, may determine how omnivorous a hoverer should be.

Leaf Top Specialization

As an alternative to the above model, our observations suggest that some species have overcome the disadvantages of *US* foraging. *Tachyphonus luctuosus*, for example, forage by moving along branches to the tips and rapidly shooting down to leaf tops exposed on the terminal ends of branches below. This strategy is particularly effective in trees (including palms) where lower branches extend

out further than higher branches. This effectively increases the visibility of US. It is the only species with which we are familiar in Panamanian forests that commonly lunges downward to attack foliage insects. *Dacnis cayana* appear to use brown areas of leaf damage as a flag to indicate potential foraging locations. On 15 occasions we observed *Dacnis* visit a tree, probe at several brown stained leaves in rapid succession, pick grubs off the spot, and leave the tree. We never saw *Dacnis* forage by searching methodically over many leaves in one tree. It is the only species for which we could detect a probably external cue on the leaves that it gleaned. Examination of larvae on these brown spots leads us to conclude that they could be attacked from the top of the leaf since leaf material is generally weak and decayed.

Leaf Top Foraging in the Canopy

From the reasoning outlined in previous sections, we outline four possible explanations for the greater amount of US foraging in the outer canopy: a) because of the increased seasonality of insects in the canopy (Karr, 1976b) the canopy supports more omnivores than committed insectivores (Greenberg, MS); these common omnivores are less proficient insectivores and use US more. b) US insects may be more common in the canopy, supporting more US foraging and species with US specialization. c) Because birds are foraging in the outer shell of vegetation, any kind of terminal branch will give birds a commanding view of a massive number of US. d) A higher proportion of orthotropic leaf arrangements, such as spiralled or decussate (Leigh, 1976), might reduce the differential in obscured vision for downward versus upward. More precise insect abundance and foraging data will be necessary to evaluate these hypotheses. Heinrich (1979) suggested that birds scrutinize more US than LS. The situation he studied, with birds foraging in the outer vegetation of small widely-spaced trees, may be analogous to the outer canopy. In these situations, visible leaf surfaces may be biased towards US.

Why Arthropods Prefer Leaf Undersurfaces

It is curious that insects sit exposed on the leaf surface that is apparently under constant scrutiny of most foliage-gleaning birds. While insects are certainly not hiding from birds on LS, they may extract an energetic cost from birds attacking them, thereby limiting the number of species of birds that can attack them. This energetic cost results from the longer average attack distance required to exploid LS arthropods. Alternatively, insects may derive an advantage for resting on LS not related to predator avoidance. Leaf bottoms may be cooler, more humid, and less exposed to wind and rain than US. It is also possible that herbivorous insects find it easier to attack a leaf from the undersurface, since it has exposed veins and is generally less cutinized and more densely perforated with stomata.

The latter hypothesis is perhaps the least likely. The preference for LS is found in many taxa and ecological groupings of arthropods. Most arthropods censused in our study were probably nocturnal and merely resting when we found them during the day. Windsor (1979), for example, found that herbivores on some legumes in Costa Rica foraged during the day, and either hid on LS or left the host plant during the day.

Whether arthropods are selecting US to avoid predators or bask in a more favorable climate is harder to discern. Four lines of evidence suggest to us the physiological advantages are most important.

1. Within insect groups, larger insects are less restricted to LS. The larger size classes are presumably preferred by most foliage-gleaning birds. Arthropods less than 2 mm, in particular, are probably rarely taken by most birds.

2. Aposomatically colored insects, which presumably have alternative predator avoidance mechanisms such as distastefulness or mimicry, show the same strong preference for LS on BCI. On the understory census we found 82% ($n=52$) of the brightly colored insects on LS. The BCI evidence is contradicted in our census data from Cerro Campana (N 8°40' W 80°04', elevation 900 m); we found relatively more brightly colored beetles on US than LS (bright insects comprised 6/17 LS and 26/36 US $\chi^2=7.0$, d.f. = 1, $p < 0.01$).

3. Insects were relatively more common on LS during the dry season on BCI. Since bird populations do not change greatly between the dry and wet season, some climatic effect seems a more reasonable explanation.

4. Insects censused at a cooler, moister mid-elevation site (Cerro Campana) showed a preference for perching on US (58% $n=101$) for arthropods > 2 mm, non-dipterans, etc.

Heinrich (1979), however, proposed that perching on leaf upper surface would promote rapid growth in caterpillars. He found well-defended or possibly noxious species to prefer leaf tops. The differences in our conclusions may result, in part, from the different study areas. After cool temperate zone nights, warm temperatures associated with leaf tops may promote caterpillars reaching optimal growth temperatures. Tropical insects may be closer to critical upper thresholds in temperature.

An additional possibility has not been considered here, for lack of information: arthropods may be avoiding predation by other arthropods. This possibility cannot be evaluated without much more information on the foraging microhabitat of major arthropod predators. While the primary advantages of LS preference in arthropods are not clear, it is not safe to assume that insects are hiding from avian predators.

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