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DEAD-LEAF FORAGING SPECIALIZATION IN TROPICAL FOREST BIRDS: MEASURING RESOURCE AVAILABILITY AND USE

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Abstract. Tropical birds foraging at dead leaves suspended above the ground in forest understory represent a system that potentially overcomes many of the difficulties inherent in measuring resource availability for insectivorous birds. Because the dead leaves are discrete and abundant resource patches, they are easily counted and sampled. I present a scheme for sampling the availability and use of specific substrate types and the abundances of arthropod prey. Availability and use are compared directly for six bird species in three habitats (upland rainforest, low-lying rainforest, and bamboo) at the Tambopata Reserve, southeastern Peru. I conclude that (1) the overall abundance, variety, and high prey productivity of dead leaves helps to maintain extreme specialization in this guild; (2) substrate types are selected nonrandomly by all species, at least partly on the basis of the differential prey availability in each type; (3) individual dead leaves are relatively long-lived and are continually recolonized by arthropods, therefore representing predictable and renewable resource patches to these birds; (4) dead-leaf specialists are exposed to distinctly different prey choices from those of birds that search live foliage. Studies of other insectivorous bird groups should include estimates of substrate availability among habitats, prey availability among substrates, as well as the use of these by the birds.

Key Words: Dead leaves; insectivorous birds; foraging specialization; resource availability.

Understanding of resource availability and distribution, as well as resource-use patterns by birds, is central to the study of foraging specialization and avian community organization. Because of difficulties in measuring arthropod abundance and actual bird diets, these are often inferred for insectivorous birds from general insect sampling, foraging behavior, and morphology. In particular, we know almost nothing of the relative productivities of specific foraging substrates and how these may vary temporally. In tropical communities these problems are often compounded by the increased number of bird species and resource dimensions.

A system that offers great potential for overcoming these difficulties is the foraging by birds among suspended dead foliage in tropical forest understory. Leaves falling from the canopy are often trapped by vines or other vegetation before reaching the ground. They persist either individually or in dense clusters, offering daytime hiding places for nocturnal arthropods. A number of tropical antbirds (Formicariidae), ovenbirds (Furnariidae), and other insectivorous species forage exclusively by extracting arthropods from within these suspended dead leaves (Remsen and Parker 1984). As many as 10–12 species of dead-leaf-searching specialists may occur with other, often congeneric, live-foliage-gleaning species in the same mixed-species foraging flocks (Munn and Terborgh 1979, Munn 1985).

The dead leaves represent abundant, yet discrete, resource patches that are easily counted and sampled for arthropod prey. This contrasts with other substrates, such as live foliage or airspace, that are more generally distributed and that may possess a diverse and highly mobile arthropod fauna. The study of such a well-defined resource system may enable us to discern details of food availability and exploitation that are generalizable to other avian insectivores.

Only one dead-leaf specialist has been studied in detail, the Checker-throated Antwren (*Myrmotherula fulviventris*) in Panama, where it is the only member of this guild (Gradwohl and Greenberg 1980, 1982a, b, 1984). Gradwohl and Greenberg demonstrated the feasibility of measuring resource availability and use for these birds, and they successfully used this foraging system to test ecological as well as behavioral hypotheses. My study of dead-leaf foraging specialization among Amazonian rainforest birds extends these findings to a multi-species assemblage that is part of the world's most diverse avifauna.

My research is aimed at determining how substrate and prey availability promote specialization and how this specialization contributes to the organization of a diverse tropical bird assemblage. In this paper, I describe and evaluate my methods for measuring resource availability and use by these birds. I also assess variability in dead-leaf distribution and prey abundance across habitats and seasons. Then, I provide evidence that individual dead leaves may represent a relatively long-lasting, renewable resource to avian insectivores. Finally, I provide examples of data on several common bird species, comparing available substrates with those actually visited by the birds. My intent is to provide a scheme for quantifying the relevant aspects of a resource system for insectivorous birds, as illustrated with data from one specialized guild.

STUDY AREA AND METHODS

Study site

This study concentrates on the Tambopata Reserve (5500 ha) in the Department of Madre de Dios, southeastern Peru (12°50'S, 60°17'W). The reserve consists of primary lowland rainforest that is typical of a vast portion of southwestern Amazonia. Several forest types are recognized and described by T. L. Erwin (1985). The bird and insect faunas also have been relatively well studied on the reserve (Parker 1982, T. L. Erwin 1985).

I worked at Tambopata from May through July 1987, covering a period from the end of the rainy season to the middle of the dry season. This region is characterized by a 5- to 6-month dry season, punctuated by occasional severe storms from the south that bring strong, cooling winds and sometimes heavy rain. The severe winds are thought to be important in maintaining a broken canopy and a prevalence of gap-inhabiting plants, including bamboo (T. L. Erwin 1985).

My study centered on three habitat types: upland forest, low-lying forest, and bamboo thickets. The upland forest (Upland Type II of T. L. Erwin 1985) is situated on sandy, relatively well-drained soils on ancient alluvial terraces high above the current river levels. This forest has a relatively closed 35- to 40-m canopy and a relatively open understory. Midstory palms and *Cecropia* spp. trees are conspicuously lacking; however, shrub-like understory palms (e.g., *Geonoma* spp.) are common. Low-lying forest (Upland Type I of T. L. Erwin 1985) is the most abundant forest type on the reserve. It occurs on poorly drained clay soils and has an uneven canopy of 30 to 35 m. Subcanopy palms (e.g., *Iriartea* spp., *Socratea* spp.) and *Cecropia* spp. are common, and the understory is often dense with vine tangles and other low vegetation. In places, the understory of this forest consists of nearly pure, dense thickets of bamboo (*Guadua* spp.) that may reach a height of 8–10 m. Primarily because the avifauna associated with this bamboo is often quite distinct from that in the surrounding forest (Parker 1982), I consider the bamboo to be a separate habitat type.

Foraging behavior

The following data were recorded with a microcasette on foraging birds encountered opportunistically on the study site: species, sex and age (if determined), habitat type, height above ground, height of tree, canopy height (all heights estimated to the nearest 1 m), foraging method (e.g., glean, probe), foraging substrate (including specific characteristics, such as leaf size and type), perch type (if different from substrate), and foliage density estimated in a 1-m radius sphere around the bird (scale, 0–5). All dead leaves were further categorized as to type (curled, tattered, or entire), and I noted their position in the vegetation (for example, in vine tangle, suspended from live branch).

Because most species of interest foraged in mixed-species flocks that I could frequently follow for extended periods, I was often able to make repeated but nonconsecutive observations of individuals by rotating my attention among the flock members. In most cases, I recorded 3–5 consecutive foraging attempts before moving on to the next bird, although I did not eliminate longer bouts by species that were difficult to observe.

Dead-leaf abundance

Numbers and distribution of suspended dead leaves were assessed at the end of the rainy season in mid-May and again in July, at the middle of the dry season. I established 10-m line transects perpendicular to existing trails at randomly assigned points, with 10 transects in each habitat type. On each transect, I counted and recorded the size (length and width, estimated to the nearest 1 cm) and type of all dead leaves encountered along a 1-m wide strip, up to 10 m above ground. All palm, *Cecropia,* bamboo, and other "novel" leaf-types were tallied separately. Leaves above 5 m were usually inspected with binoculars. Using these methods, 100 m^3 of the forest understory were sampled, with data recorded separately for each horizontal and vertical 1-m interval. These data yielded the number and surface area (length × width) of dead leaves per cubic meter, with associated variances representing horizontal and vertical patchiness for each plot. Because leaf density was usually high, a large sample of leaf sizes and types was also obtained.

Arthropod abundance

Arthropods were sampled from individual dead leaves collected in areas adjacent to the leaf-sampling transects. For each sample, the first 30–50 leaves encountered within reach, and removable without disturbance, were placed individually into zip-lock plastic bags. Because most arthropods were reluctant to flush from the leaves, escape was minimal. After being killed with insecticide (Raid®), arthropods were separated from the leaves, classified to order, measured to the nearest 1.0 mm, and preserved in 70% ethanol. These voucher specimens will be identified later to lower taxonomic levels, if possible, and deposited at the LSU Entomology Museum. To relate substrate characteristics to arthropod numbers and type, I recorded the size and type of each leaf sampled.

To compare arthropod frequency on live vs. dead leaf substrates, these samples were supplemented with visual searches of an equivalent number of live leaves in the same areas. The type and size of all arthropods encountered on leaf surfaces were recorded during slow passes through understory vegetation, sampling all consecutive leaves clearly visible (upper and lower surfaces) without disturbing the foliage.

Temporal changes in resource availability

As noted above, seasonal change in dead-leaf abundance was assessed on transects censused in May and July 1987. In addition, I individually marked all dead leaves on 2 × 2 × 2-m plots and checked these weekly throughout the season (7–8 weeks) to measure persistence and local accumulation. I established three plots in low-lying forest, two in upland forest, and two in bamboo. These were supplemented by marking additional *Cecropia* leaves and other large leaves that were under-represented on the plots. A total of 1022 leaves was marked, including those recruited into the plots during the study.

TABLE 1. CHARACTERISTICS OF DEAD-LEAF FORAGING BIRDS AT THE TAMBOPATA RESERVE, SOUTHEASTERN PERU. HABITATS ARE UPLAND FOREST (U), LOW-LYING FOREST (L), AND BAMBOO (B)

Species	Body wt. (g)[a]	Habitat	Percent use of dead leaves	Number of foraging observations
Olive-backed Foliage-gleaner	38.8	U	90	124
Brown-rumped Foliage-gleaner	30.7	L, B	97	231
Buff-throated Foliage-gleaner	33.8	L	98	132
Ornate Antwren	9.5	L, B	99	227
White-eyed Antwren	9.3	L, B, U	99	693
Moustached Wren	18.5	B	96	52

[a] Mean of five male and five female specimens.

Finally, to assess turnover and colonization of arthropods at individual leaves, I used a sample of 45 leaves that were easily checked with minimal disturbance. These were monitored every 1–2 days for arthropod inhabitants, for a total of 1305 checks. If the arthropod remained in the leaf (58% of visits), I noted the number of consecutive visits on which it was present. If the arthropod flushed from a leaf during a check, I recorded the time until that leaf was reoccupied. Thus, I simultaneously measured changes in occupancy under conditions of disturbance (perhaps simulating predation) and lack of such disturbance.

RESULTS

AVIAN DEAD-LEAF SPECIALISTS

Data are presented for six bird species that foraged heavily on dead leaves at Tambopata (Table 1). For each species, more than 90% of my observations were at dead-leaf substrates within 10 m of the ground, allowing appropriate comparisons with resource availability measurements. Two additional species of dead-leaf specialists occurred in the understory at Tambopata, but were less common, and up to seven specialists foraged in the subcanopy and canopy.

Antwrens in the genus *Myrmotherula* traveled almost exclusively in mixed-species understory flocks, feeding actively at individually suspended leaves. They often employed acrobatic maneuvers, such as extended reaches or clinging at the tips of leaves, to inspect each leaf carefully for arthropods. The White-eyed Antwren (*M. leucophthalma*) was a habitat generalist at Tambopata, occurring in nearly every foraging flock in all three habitat-types. The Ornate Antwren (*M. ornata*) was restricted to low-lying forest in the vicinity of bamboo (see also Parker 1982) but foraged both inside and away from bamboo thickets.

The larger foliage-gleaners (*Automolus* spp.) also traveled in the same mixed-species flocks, usually moving deliberately along branches or in vine tangles. They probed into individual large leaves or frequently investigated dense clusters of leaves lodged among vines or live foliage. Occasionally, these birds manipulated the substrates with their bills, for example, by picking leaves from a cluster and then dropping them to the ground. Both the Buff-throated (*A. ochrolaemus*) and the Brown-rumped (*A. melanopezus*) foliage-gleaners occurred widely in the low-lying forest, sometimes feeding side by side in the same flocks. All flocks with Brown-rumped Foliage-gleaners were in the vicinity of bamboo thickets and this species is considered a bamboo specialist by Parker (1982) and Terborgh et al. (1984). However, I rarely observed it foraging within bamboo foliage. The Olive-backed Foliage-gleaner (*A. infuscatus*) was largely restricted to the upland forest and more open areas in the low-lying forest far from bamboo.

The sixth species considered here, the Moustached Wren (*Thryothorus genibarbis*), occurred primarily in dense, low, river-edge forest and bamboo thickets. In bamboo, this species foraged in solitary pairs in dense clusters of dead leaves and debris, or at individual large *Cecropia* leaves suspended in dense live foliage. Pairs only temporarily joined mixed-species flocks that passed through their territories.

Species-specific comparisons with respect to foraging height and use of particular dead-leaf types will be presented elsewhere (Rosenberg, unpubl.). In general, species differed most in their use of those leaf types, such as palms, *Cecropia*, and bamboo, that were specific to each habitat. Importantly, no species in any habitat searched leaves classified as entire (<1% of all observations).

DEAD-LEAF ABUNDANCE

The overall height distribution and average density of dead leaves were similar in the three habitats, with most leaves concentrated in the first 3 m above the ground (Fig. 1). Individual transects varied considerably in abundance, however, with density ranging from 2.6/m^3 to 8.7/m^3.

Between May and July, abundance of leaves increased about 50% in two of the three habitats, a difference greater than that between any habitat

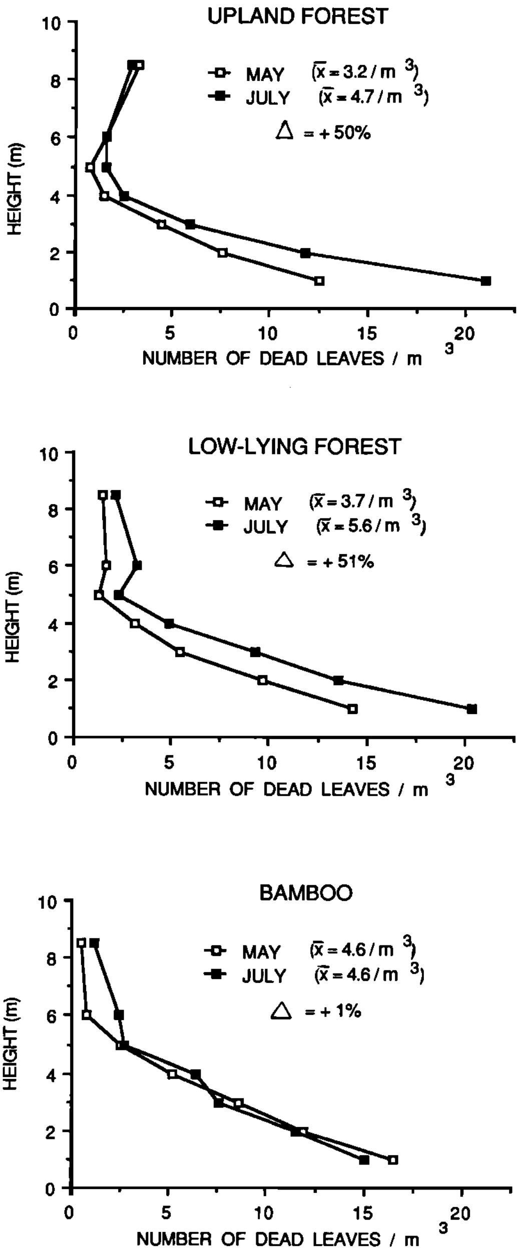

FIGURE 1. Abundance and height distribution of dead leaves in three habitats at Tambopata in May and July 1987 ($\bar{X}$ = average leaf density on 10 transects in each habitat; Δ = percent change in leaf density between May and July).

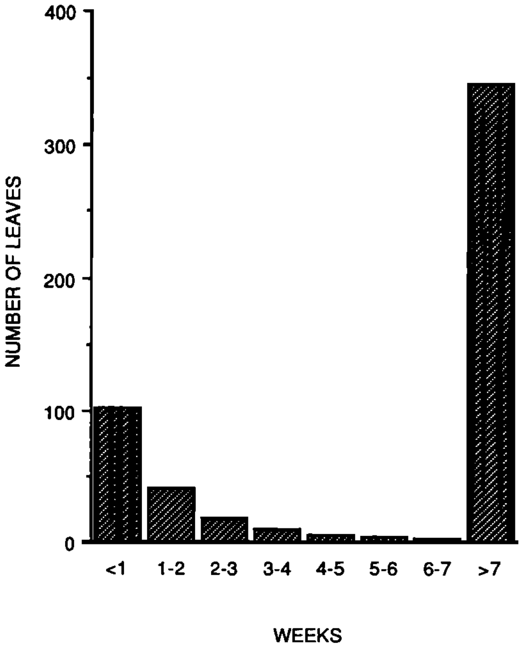

FIGURE 2. Persistence of suspended dead leaves at Tambopata (data from 1022 marked leaves on seven plots in three habitats).

types in a single season (14–30%). The steady accumulation of trapped leaves throughout the early dry season was also apparent in the plots with marked leaves. The net number of leaves increased on all plots (36–294%), with the largest increases in upland forest and the smallest in bamboo. The longevity of individual leaves exhibited a bimodal pattern in all three habitats (Fig. 2), with leaves either disappearing shortly after falling or remaining for long periods. Because I could not determine when leaves present at the beginning of the study had first fallen, or when leaves present at the end of the study eventually disappeared, these represent minimum estimates of longevity. However, I can be certain that of all leaves recruited onto the plots during the study period, 20% disappeared in the first week. Similarly, 66% of all leaves marked at the beginning of the study were still present 7 to 8 weeks later.

DISTRIBUTION OF SUBSTRATE TYPES

The distribution of sizes and types of dead-leaf substrates differed greatly among the habitats (Fig. 3). The average leaf size was highest in low-lying forest and lowest in upland forest. In general, leaf sizes exhibited a bimodal pattern with 8- to 10-cm leaves always most abundant, and with the largest leaves in each habitat being "novel" leaves associated with that habitat. For example, understory palm leaflets were numerous in upland forest, larger palm fronds (e.g., *Iriartea* spp.) were common in low-lying forest, and bamboo and *Cecropia* leaves dominated in bamboo thickets. Upland forest also had the

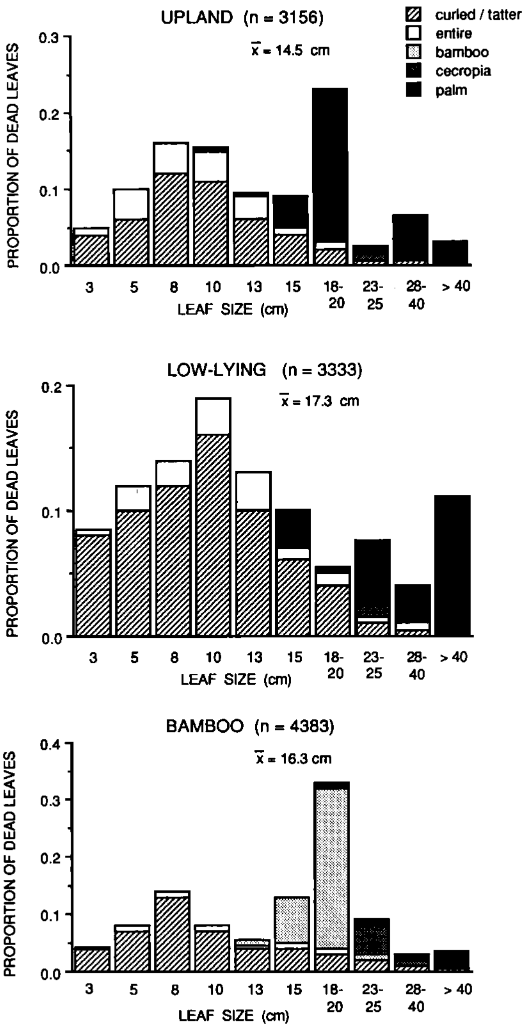

FIGURE 3. Distribution of dead-leaf sizes and types in three habitats at Tambopata in May 1987 ($\bar{X}$ = average leaf size).

greatest proportion of entire leaves (18%). Mean leaf size increased with height above ground in each habitat, as did the proportion of novel and other large leaves in low-lying forest and bamboo.

Prey Availability

During May, a total of 1000 dead leaves was sampled for arthropods in the three habitats (Table 2). Prey density ranged from 0.39/leaf in low-lying forest to 0.53/leaf in bamboo. In July, the density of arthropods in 200 dead leaves in low-lying forest was 0.30/leaf. These estimates excluded a large number of 1- 3-mm social ants and their nests concentrated in fewer than 10 leaves (each nest counted as one prey item). In contrast, a search of 810 live-leaf surfaces in low-lying forest in May yielded 0.18 arthropods/leaf. The differences between live- and dead-leaf substrates were even more apparent when the sizes and taxa of the arthropods were considered. Dead-leaf arthropods averaged significantly larger (6.5 mm vs. 3.8 mm, $P < 0.001$, Mann Whitney U-test; Fig. 4). Over 75% of the arthropods on live leaves were 2–4 mm in length and none was >10 mm. In dead leaves, 53% of the arthropods were >5 mm and 16% were >10 mm long. Similarly, nearly two-thirds of the live-leaf arthropods were conspicuously colored ants, flies, and wasps, whereas these made up <10% of the dead-leaf samples. Over two-thirds of the dead-leaf arthropods were cryptically colored beetles, roaches, orthopterans, and spiders (Fig. 5).

TABLE 2. Prey Densities on Live and Dead Leaf Foliage at Tambopata Reserve

Habitat	Leaf type	Month	Arthropod density (number/leaf)	Number of leaves
Upland forest	dead	May	0.41	380
Bamboo	dead	May	0.53	300
Low-lying forest	dead	May	0.39	320
Low-lying forest	dead	July	0.30	200
Low-lying forest	live	May	0.18	810

The number of arthropods per dead leaf increased sharply with increasing leaf size ($r = 0.944$, $P < 0.01$; Fig. 6). This trend was evident in each of the three habitats. Very small (3–8 cm) leaves and entire leaves had the lowest frequency of arthropods, whereas prey density was extremely high in leaves >40 cm long (regardless of type) and in *Cecropia* leaves (regardless of size). Bamboo and palm leaflets had arthropod densities slightly below the overall average.

Overall, individual dead leaves had a high rate of turnover and renewal of arthropods. Most arthropods that I did not flush remained in a given leaf for only 1–2 days ($\bar{X}$ = 1.66, Fig. 7). A few leaf inhabitants stayed longer, however, with the longest being a roach present on nine consecutive visits (12 days) to the same leaf. Given that an arthropod remained in a leaf after a visit, there was a 39% chance of it being there on the next visit, a 44% chance of that leaf being empty, and a 17% chance of a different arthropod being present. In cases in which an arthropod flushed from a leaf, most leaves were reoccupied on the second or third subsequent visit (Fig. 8). In these cases there was a greater chance of the leaf being empty on the next visit (73%); on 16% of my visits, a different arthropod was present.

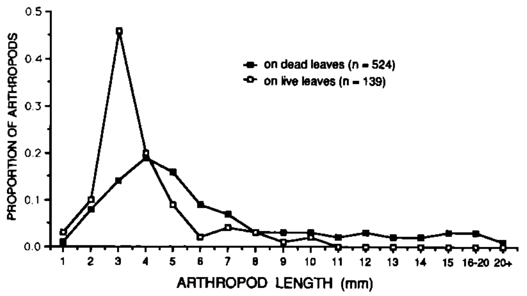

FIGURE 4. Size distribution of arthropods on live and dead leaves at Tambopata.

USE VS. AVAILABILITY

Here, I compare the distributions of dead-leaf sizes and types used by the birds with those available in the appropriate habitats. In this way, I can separate selectivity and avoidance of particular substrate types from simple use. All species selected leaves differently from their availability in their respective habitats (Fig. 9), and all of these differences were highly significant (Kolmogorov-Smirnov and Chi-squared tests; $P < 0.001$). In general, all species selected larger and certain novel types of leaves, and they avoided the smallest leaves in each habitat. Use of *Cecropia* leaves by most species was much greater than their availability, although these leaves were probably under-represented in the transect samples. However, heavy use of some leaf types did not always represent selectivity. For example, use of understory palm leaflets by White-eyed Antwrens in upland forest and of larger palm fronds by Buff-throated Foliage-gleaners in lowlying forest were almost exactly equal to their availability in these two habitats.

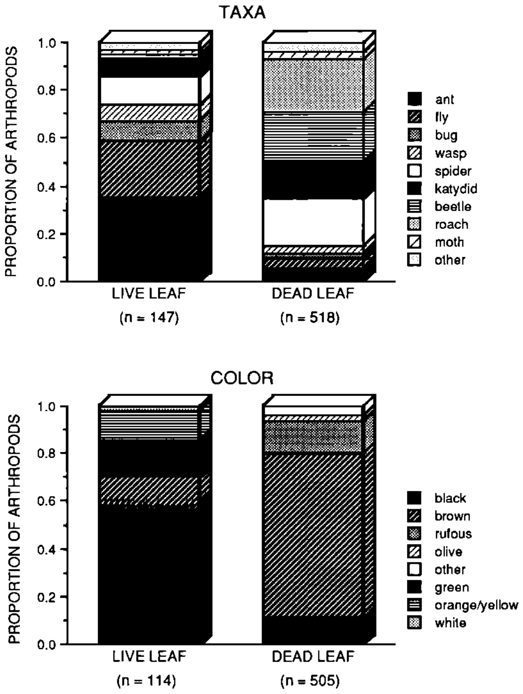

FIGURE 5. Characteristics of arthropods on live and dead leaves at Tambopata.

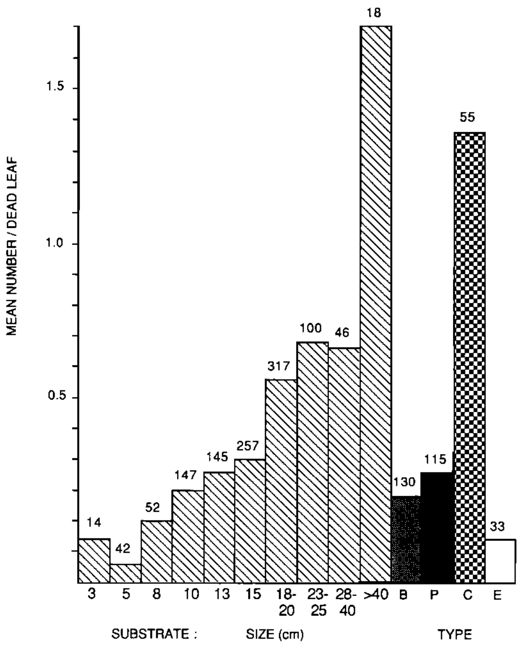

FIGURE 6. Mean number of arthropods in dead leaves of different size and type (B = bamboo, P = palm, C = *Cecropia,* E = entire). Number of leaves sampled, by category, are shown above each bar.

To see if selectivity could be explained by the prey productivity of the different sized leaves, I weighted the leaf-availability distribution by the frequency of arthropods in each leaf type (from Fig. 6) and again compared these with substrate use by the birds. Differences were still significant for all species comparisons, except that in most cases use of the very small leaves was now nearly equal to their weighted availability. Thus, low prey density probably explains the avoidance of these small leaves (and of entire leaves), but the larger, and especially *Cecropia,* leaves were still searched more than expected.

DISCUSSION

The empirical data presented here center on one important aspect of the food resource, namely foraging substrate. The exact substrates from which insectivorous birds obtain their prey are

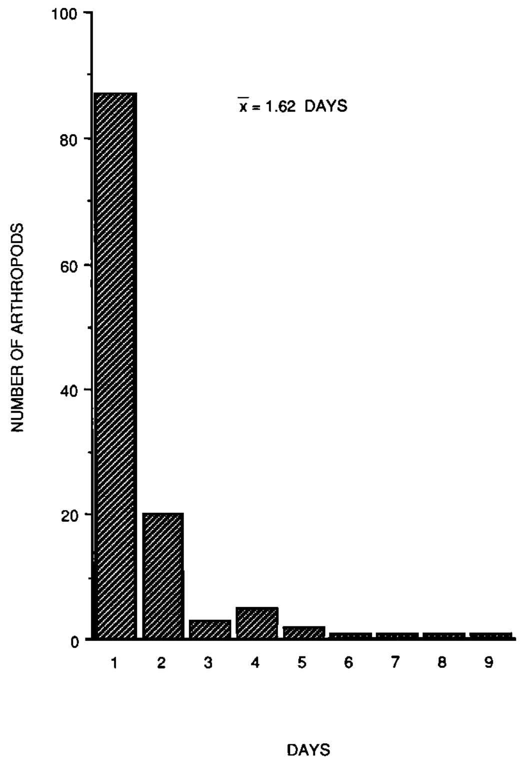

FIGURE 7. Length of stay by arthropods in individual dead leaves at Tambopata (based on sequential checks of leaves from which arthropods did not flush).

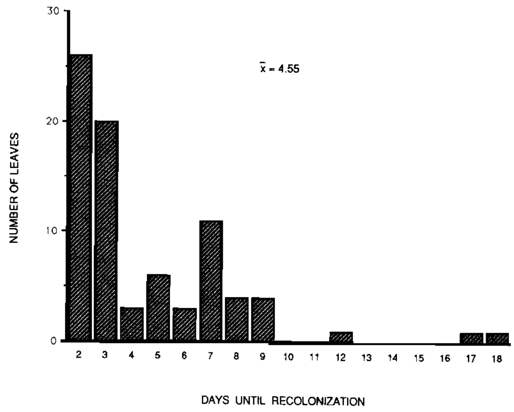

FIGURE 8. Time until recolonization by arthropods at individual dead leaves at Tambopata (based on sequential checks of leaves from which an arthropod had previously flushed).

usually used to define subgroups or guilds within avian communities (e.g., Root 1967, Holmes et al. 1979b). It is largely through substrate choice that prey availability is mediated. It is also likely that overall habitat and foraging-site selection is determined in part by the distribution and productivity of specific foraging substrates. A higher degree of resource specialization and, in particular, substrate subdivision is thought to be one mechanism promoting the higher species diversity in tropical vs. temperate bird communities (Orians 1969b; Karr 1971, 1976; Terborgh 1980a; Remsen 1985). However, critical evaluations of substrate use, even for most temperate communities, are lacking. Substrates are usually measured only in a general way (e.g., bark, foliage, ground), and studies of the arthropod prey available on specific substrates are rarely attempted.

By sampling the availability of particular dead-leaf substrates, I was able to identify finer levels of resource segregation within a guild that was already considered highly specialized with regard to substrate. More importantly, I was able to distinguish between substrate types selected and simple use. Furthermore, by sampling the prey productivity of the individual substrate types, I was able to explain at least part of the observed selectivity. Thus, I can conclude that all species in my study selected foraging sites nonrandomly, avoiding the least productive substrates. Greenberg and Gradwohl (1980) also emphasized the importance of more subtle distinctions in substrate type by demonstrating a large difference in prey availability and avian use between upper and lower leaf surfaces in a Panamanian forest.

In general, this level of understanding has only been possible in studies of guilds such as frugivores or nectarivores in which resources are clearly defined and can be measured precisely. In such studies, the relationship between food availability and community organization has been demonstrated, as has the potential for coadaptation between plants and their specialized avian pollinators (Feinsinger and Colwell 1978, Stiles 1985c) and seed-dispersers (Howe 1977, Moermond and Denslow 1985). Could such strong interactions exist between avian insectivores and their prey? The answer must begin with a detailed knowledge of the distribution and availability of arthropods and their selection by birds exploiting specific foraging sites.

The present study provides clear evidence that birds foraging on dead vs. live foliage are exposed to very different prey choices (cf. Gradwohl and Greenberg 1982a and Greenberg 1987a). The significance of these differences can be assessed, however, only through direct examination of species' diets. Preliminary analysis of stomach contents of several dead-leaf specialist birds from my study areas (Rosenberg, unpubl. data) indicates heavy predation on those taxa (e.g., Orthoptera, spiders) that were most abundant in my dead-leaf samples.

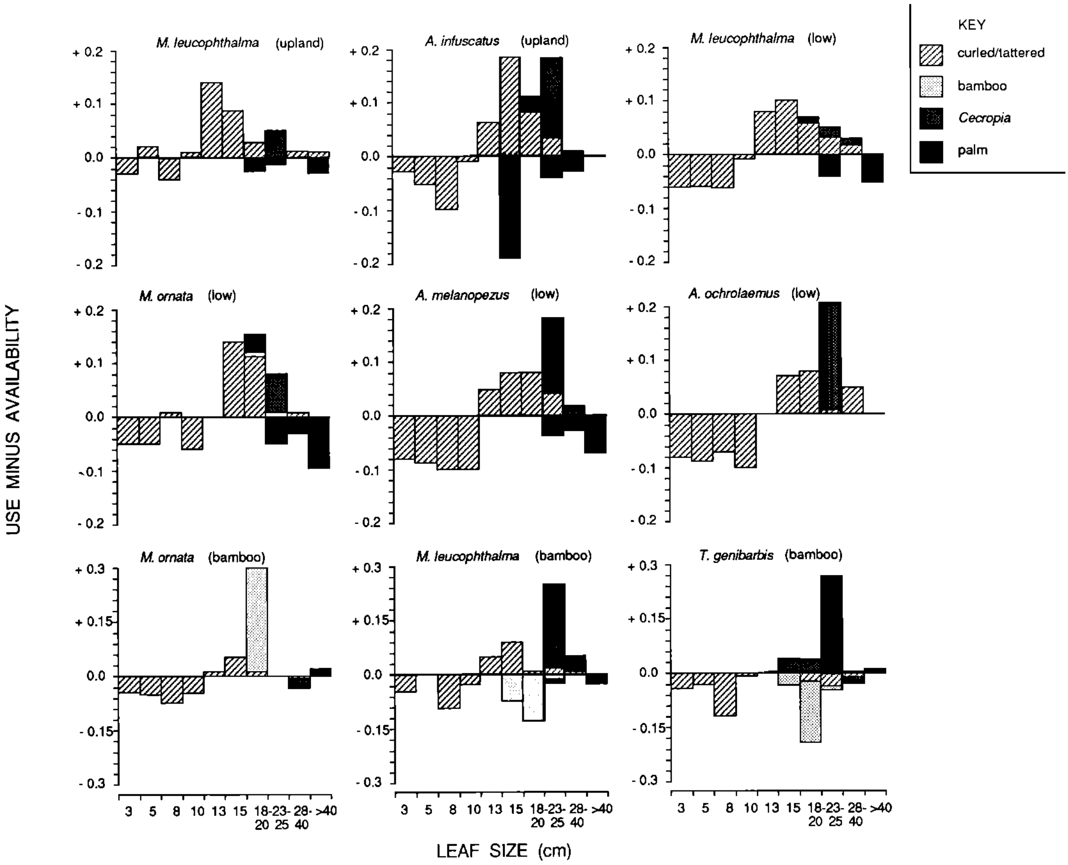

FIGURE 9. Selectivity of dead-leaf substrates by six bird species in three habitats at Tambopata (data are the proportional use of each category by the bird in relation to the availability of that category in that habitat). Bars above the horizontal represent selection and bars below represent avoidance of each category.

For sedentary, permanent-resident birds, foraging specialization may be enhanced where resources exist in predictable patches. The persistence of individual dead leaves and the turnover rates of potential prey in these leaves suggest that antwrens and foliage-gleaners may perceive these leaves as predictable and renewable resources. I suggest that the birds recognize particular leaves within their territories and visit them repeatedly.

Are the patterns discussed here unique to a novel tropical resource or do they have more general applicability for insectivorous birds? To answer this question we require more detailed prey sampling and more detailed observation of substrate and prey choice than has been done to date. For many North American insectivore guilds, for example, we know much about general foraging relationships among species, but we know little about specific diets, how these vary temporally, or how these may be mediated by the differential productivity of specific foraging sites. Certainly, guilds vary in their degree of specialization and the extent to which food availability promotes species interactions. A study design that assesses the relationship between resource availability and use is necessary to address these questions in any system. It should begin with close attention to natural history, so that levels of resource subdivision important to the birds can be determined. The relevant categories of substrate subdivision can then be sampled for potential arthropod prey. In this way, the distribution of specific foraging substrates among the available microhabitats, as well as the relative productivity of each substrate type, can be determined. All these measures may vary geographically and temporally, necessitating replicate samples.

This approach will be easier to apply in cases in which substrates occur in discrete patches, such as the dead leaves. In other systems, innovative methods may be sought to isolate and sample specific substrates. For example, individual live leaves, or branchlets, or flower clusters may be collected or examined for arthropods. This is preferable to more general measures of productivity, such as those obtained from light traps or sweep-netting. In addition, other exceptional resource systems that allow more precise measurements may be exploited. For example, among tropical forest birds, some species appear to specialize on epiphytes or vines, or specific plant species such as bamboo. Many North American birds may also prefer specific foraging surfaces. Only by building an empirical base for a variety of species can the generality of the conclusions from this one specialized guild be assessed.

There are limitations to the approach I have outlined. Although comparisons of use and availability suggest patterns of selectivity and factors that may lead to specialization, questions involving behavioral preferences, plasticity, and the role of interspecific interactions may not be answered by observations, but may require experimental testing. The same resource systems that allow direct sampling of availability and use may also lend themselves to experimental manipulation. For example, based on my studies at Tambopata, I have devised a series of tests involving the manipulation of dead-leaf types and prey. These will assess the flexibility of observed behaviors and the relative efficiencies (i.e., competitive ability) of specialists vs. nonspecialists at particular foraging substrates. It is possible, for instance, that some live-foliage-gleaning species may actually prefer dead leaves but are excluded from this resource by the more efficient specialists.

In summary, I have provided an example of a resource system that may be used to overcome many of the difficulties typically encountered in studies of insectivorous birds. By sampling the distribution, productivity, and exploitation of discrete resource patches, I am able to make the following conclusions regarding dead-leaf foraging specialization: (1) the overall abundance, variety, and high prey productivity of dead leaves has promoted extreme specialization within this guild; (2) substrate types are selected nonrandomly by all species, at least partly on the basis of their differential arthropod availability; (3) individual dead leaves are relatively long-lived and may represent predictable and renewable resources to these birds; (4) dead-leaf specialists are exposed to distinctly different prey choices from those of birds that search live foliage. Assessing the generality of these conclusions awaits the application of a substrate-based sampling approach to a variety of other insectivorous bird groups.

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