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Author(s): Kenneth V. Rosenberg

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## ECOLOGY OF DEAD-LEAF FORAGING SPECIALISTS AND THEIR CONTRIBUTION TO AMAZONIAN BIRD DIVERSITY

KENNETH V. ROSENBERG

*Museum of Natural Science, Foster Hall 119, Louisiana State University, Baton Rouge,  
Louisiana 70803, USA*

*Present address: Cornell Lab of Ornithology 159 Sapsucker Woods Rd. Ithaca,  
New York 14850, USA*

**ABSTRACT.**—One reason suggested for the high avian species diversity in tropical forests is increased specialization on resources that are absent in temperate habitats. This study investigates in detail one such specialization, namely foraging for arthropods in suspended aerial leaf-litter in lowland tropical rainforest. Up to 16 species at two southwestern Amazonian sites constitute a guild of specialized dead-leaf foragers that make up roughly 11% of the region's insectivorous bird species. Most dead-leaf specialists are ovenbirds (Furnariidae) or antbirds (Formicariidae) that are characteristic members of mixed-species foraging flocks in the understory or canopy. These specialists, compared with other insectivores, tended to use more acrobatic postures and manipulated foraging substrates with the bill or feet. These species segregated to some extent by habitat, including several congeneric replacements. The guild reaches its highest diversity in a belt across southwestern Amazonia and along the base of the Andes, where bamboo and other disturbance-related microhabitats add to forest heterogeneity. Individual dead leaves, as resources for birds, were abundant in all forest types and supported higher prey densities (number per leaf) than adjacent live foliage. Prey density was highest in larger leaves, especially in large, crumpled *Cecropia* leaves. The arthropod fauna of aerial leaf-litter was similar among seasons, habitats, and sites, being dominated by spiders, roaches, other orthopterans, and small beetles. This contrasts greatly with arthropods available on live foliage. Guild members differed significantly from each other in either foraging height, size or type of leaves searched, diet composition, or prey size, although overlaps between species pairs were usually high ( $\geq 0.900$ ). Although twice as many species were supported in low-lying forest than in upland forest, ecological overlaps among species in each habitat were usually similar. Behavioral similarity among species was not related to dietary overlap. Size of prey taken, however, was correlated with bill size, except that the largest species, *Xiphorhynchus guttatus*, ate surprisingly small prey. Diet composition of all species differed significantly from prey availability in dead leaves, with orthopterans selected by all species and small roaches and spiders often avoided. Censuses of 92 mixed-species flocks revealed no negative and only two positive associations between species, suggesting that birds join flocks independent of other species present. Co-occurring *Myrmotherula leucophthalma* and *M. ornata* in the same flocks were not aggressive and converged in foraging height and substrate use. In contrast, co-occurring *Automolus* foliage-gleaners tended to diverge in foraging height and exhibited overt aggression. Niche segregation among dead-leaf foragers therefore represents a balance between benefits and constraints imposed by feeding in a mixed-species flock; that is, increased vigilance and group defense of territories versus feeding close to potential competitors. Dead-leaf specialization evolved independently in several bird families but shows strong phylogenetic constraints among genera. Phylogenetic study of *Myrmotherula* antwrens revealed that all specialist species were related and that they have been evolving separately from other antwrens perhaps for as long as nine million years. Foraging specialization is therefore a primitive trait within this group (and probably others), appearing before the radiation of modern species. Study of present-day ecology may not elucidate factors leading to the evolution of such specialization, especially without concurrent phylogenetic analyses.

**RESUMEN.**—Una de las razones sugeridas para la gran diversidad de aves en los bosques tropicales es el aumento en la especialización sobre recursos que están ausentes en hábitats templados. Este estudio investiga en detalle una de tales especializaciones, esto es, el forrajeo para artrópodos en hojarasca suspendida en bosques tropicales de tierras bajas. Hasta 16 especies de aves en dos sitios en el suroeste de Amazonia con-

stituyen un tipo de forrajeadores especializados en la hojarasca, los cuales forman aproximadamente el 11% de las especies de pájaros insectívoros de la región. La mayoría de los especialistas en hojarasca son pizpitás (Furnariidae) o pájaros comehormigas (Formicariidae), que son miembros característicos de bandadas mixtas de forrajeo en el sotobosque o el dosel. Estos especialistas, comparados con otros insectívoros, tendieron a colocarse en posturas más acrobáticas y a manipular el sustrato de forrajeo con las patas o el pico. Estas especies se segregaban por hábitat, hasta cierto punto, incluyendo varios congéneres que les reemplazaban. Esta asociación alimentaria alcanzó su mayor diversidad en la faja a través del suroeste de Amazonia y a lo largo de la base de los Andes, donde las bambúas y otros microhabitats de áreas perturbadas le añaden heterogeneidad al bosque. Hojas muertas individuales, como recurso para los pájaros, eran abundantes en todos los tipos de bosque y sostuvieron una mayor densidad de presas (número por hoja) que el follaje vivo adyacente. La densidad de presas fue mayor en hojas más grandes, especialmente en las hojas arrugadas grandes de *Cecropia*. La fauna artrópoda de la hojarasca suspendida fue similar a través de las estaciones del año, hábitats, y sitios, siendo dominada por arañas, cucarachas, otros ortópteros y escarabajos pequeños. Esto contrasta grandemente con los artrópodos disponibles en el follaje vivo. Miembros de las distintas asociaciones alimentarias difirieron significativamente uno del otro en altura de forrajeo, tamaño o tipo de hojas forrajeadas, composición de la dieta, o el tamaño de la presa, aunque los solapamientos ecológicos entre parejas de especies fueron usualmente altos ( $\geq 0.900$ ). Aunque se encontró el doble de especies en terrenos bajos comparados con bosques en terrenos altos, el solapamiento ecológico entre las especies en cada hábitat fue usualmente similar. La similaridad en el comportamiento entre especies no estuvo relacionada con el solapamiento dietético. El tamaño de las presas cazadas, sin embargo, estuvo correlacionado con el tamaño del pico, excepto que la especie más grande *Xiphorhynchus guttatus*, consumió presas sorpresivamente pequeñas. La composición dietética de todas las especies difirió significativamente de la disponibilidad de presas en hojas muertas, siendo los ortópteros seleccionados por todas las especies, mientras que cucarachas y arañas pequeñas fueron evitadas. Censos de 92 bandadas de especies mixtas no revelaron asociaciones negativas y solamente dos asociaciones positivas entre especies, lo que sugiere que las aves se asocian con bandadas independientemente de qué otras especies estén presentes. Individuos de *Myrmotherula leucophthalma* y *M. ornata* que se encontraban en las mismas bandadas no eran agresivos y convergían en la altura y substrato utilizado. En contraste, *Automolus* tendió a divergir en la altura de forrajeo y exhibió agresión abiertamente. La segregación de nichos entre forrajeros de hojas muertas, por lo tanto, representa un balance entre beneficios y costos impuestos por alimentarse en bandadas de especies mixtas; esto es, aumento en la vigilancia y la defensa grupal de territorios versus la alimentación cerca de competidores potenciales. La especialización en hojas muertas evolucionó independientemente en varias Familias de aves, pero muestra fuertes restricciones filogenéticas entre Géneros. El estudio filogenético de *Myrmotherula* reveló que todas las especies especialistas estaban relacionadas y han estado evolucionando separadamente de otros del mismo Género, quizás por tanto como nueve millones de años. La especialización en el forrajeo, por lo tanto, es un rasgo primitivo dentro de este grupo (y probablemente otros), que aparece antes de la radiación evolutiva de especies modernas. El estudio de la ecología actual puede no elucidar factores que conlleven a la evolución de tal especialización, especialmente sin los análisis filogenéticos correspondientes.

Specialization on food resources that are unique to tropical habitats has been suggested as a major mechanism promoting high avian diversity in tropical versus temperate regions (Orians 1969, Karr 1971, 1976; Terborgh 1980, Remsen 1985). Examples of specialized tropical birds include those restricted to localized habitats such as bamboo and river-edge forests, those foraging exclusively on novel substrates such as epiphytic plants, vine tangles, and suspended dead foliage, those relying year-round on nectar or fruit, and those species that rely on other organisms such as army ants or monkey troops to flush their prey. This study investigates one of these novel specializations, namely the extraction of arthropods from curled dead leaves suspended above the ground in tropical forests.

In many tropical forests, leaves falling from the canopy are trapped before reaching the ground by vines and other understory vegetation, forming an aerial leaf-litter. These suspended dead leaves are used as diurnal hiding places for nocturnal arthropods, such as roaches, katydids, beetles, and spiders. A number of bird species have been shown to forage exclusively by searching for arthropods in these dead leaves (Gradwohl and Greenberg 1984, Remsen and Parker 1984, Rosenberg 1990a, 1993).

This specialized foraging system is of interest for two reasons. First, it is virtually absent outside of Neotropical forest communities and therefore may contribute significantly to increased avian species diversity in these communities. Second, because the dead leaves represent discrete resource patches that are easily quantified and sampled for arthropod prey, resource availability and use can be directly measured and compared (Gradwohl and Greenberg 1982a,b; Rosenberg 1990a). This contrasts with many other situations in which arthropods may move among a variety of microhabitats. Studies of insectivorous bird communities often have been hampered by the difficulties in measuring such mobile prey resources.

The 11 species of dead-leaf specialists listed by Remsen and Parker (1984) are members of two exclusively Neotropical families, the ovenbirds (Furnariidae) and antbirds (Formicariidae). Members of these families have been observed foraging in dead leaves as far north as southern Mexico (Slud 1964; Skutch 1972, 1982; Alvarez del Toro 1980), but their degree of substrate specialization has not been studied. In addition, a variety of other species may regularly use dead-leaf substrates, including barbets (Capitonidae), woodcreepers (Dendrocolaptidae), wrens (Troglodytidae), tanagers (Thraupinae), and blackbirds (Icterinae) (Remsen and Parker 1984). Some North American wood-warblers (Parulinae) use dead leaves to some extent on their wintering grounds (Morton 1980, Remsen and Parker 1984, Remsen et al. 1989), and one species, *Helmintheros vermivorus*, is a specialist on dead leaves in winter (Greenberg 1987a,b).

Detailed studies of *Myrmotherula fulviventris* in Panama, where it is possibly the only member of this guild (Gradwohl and Greenberg 1980, 1982a, 1982b, 1984), concluded that this species: (1) spent 98% of its foraging time searching curled dead leaves; (2) was able to reduce populations of its preferred prey (orthopterans and spiders) by 50% over a 6-wk period; and (3) was most successful at longer, highly curled leaves, which contained significantly more arthropods. Closely related *Myrmotherula* species in South America show similar degrees of specialization (98–99% of observations; Rosenberg 1993).

In Amazonia, where up to 10–15 dead-leaf foraging species may co-occur locally, the potential for interactions among guild members is enhanced because these birds are characteristic members of mixed-species foraging flocks in the forest understory or sub-canopy (Munn and Terborgh 1979, Munn 1985). Some species are known to defend year-round territories against conspecifics in neighboring flocks, and they frequently travel and forage together with congeners or other flock members that search live foliage or other substrates. Comparisons among dead- and live-leaf foraging antwrens (Rosenberg 1993) revealed that substrate specialization resulted from fundamental differences in search behavior. Remsen and Parker (1984) suggested that dead-leaf specialists may further subdivide the aerial leaf-litter resource by segregating with respect to habitat, foraging height, leaf size, or prey type.

In this paper I describe in detail the ecology of dead-leaf foraging birds at two southwestern Amazonian sites. This study addresses four questions: (1) what contribution does this specialized guild make to overall insectivorous bird diversity in Amazonia? (2) are species-specific behaviors associated with dead-leaf specialization? (3) what aspects of resource availability (including arthropod prey) serve to promote specialization? and (4) do members of this specialized foraging guild further partition the aerial leaf-litter resource?

## STUDY AREA AND METHODS

**Study area.**—I worked at two lowland sites in southwestern Amazonia. The first was the 5,500-ha Tambopata Reserve in depto. Madre de Dios, southeastern Peru (12°50'S, 69°17'W), at 290 m. General aspects of the reserve are described by Erwin (1985). This region is characterized by a distinct dry season, corresponding to the austral winter, usually from June to October. Rainfall during this period frequently accompanies southern cold fronts (*friajes*), which also usually bring high winds and temperatures as low as 10°C.

At Tambopata, I worked in three habitat types, all in primary rainforest. Upland forest (Upland type II of Erwin 1985, *terra firme* of Marra 1989) occurred on high, ancient alluvial terraces on relatively well-drained, sandy soils. Low-lying forest (Upland type I of Erwin 1985, transitional forest of Parker 1982, Marra 1989) occurred throughout the reserve on poorly drained soils; these flooded locally from high rainfall but were above the influence of fluctuating river levels. Vegetation in these forests is described further in Rosenberg (1990a), Erwin (1985), and Marra (1989). Locally within the low-lying forest, and along rivers, the understory is dominated by nearly pure stands of bamboo (*Guadua* spp.), which I consider a third habitat type. Over 20 km of trails traverse the reserve, allowing easy access to each forest type. The avifauna of Tambopata is relatively well known (Parker 1982, unpubl. data). I worked at Tambopata for 231 field-days

(5 May–20 July 1987, 28 June–15 October 1988, and 5 September–23 October 1989), covering the period from late rainy season to late dry season.

The second study site was in depto. Pando, northwestern Bolivia, 12 km SW Cobija (11°9'S, 68°51'W), at 325 m. This site was in hilly forest in the Acre-Purus drainage, about 200 km NNE Tambopata. At Pando, I worked in two habitats, upland forest and bamboo. The upland forest was similar to that at Tambopata, with a relatively open understory consisting mostly of shrub-like palms (e.g., *Geonoma* spp.) and a canopy of 30–40 m. This forest was dissected by streams, along which grew dense thickets of bamboo. The bamboo here was spineless and structurally different from that at Tambopata. I worked at the Pando site from 9 June to 8 August 1986 (mid-dry season) as part of a general avifaunal survey conducted by Louisiana State University Museum of Natural Science (LSUMNS; Parker and Remsen 1987).

**Resource use and degree of specialization.**—To ascertain degree of specialization and associated behaviors, I attempted to quantify the foraging behavior of all arboreal insectivorous species at each study site. I observed foraging birds primarily by first locating mixed-species foraging flocks in each habitat and then following these for as long as possible. The vast majority of observations were made before 1200 h. I recorded data on all species and noted flock compositions, but I concentrated my observations on dead-leaf foraging species. To minimize consecutive observations, I rotated my attention among flock members.

For each foraging individual, I recorded onto microcassette: height above ground, canopy height, foraging site (e.g., vine tangle, live branch), relative foliage density (scale, 0–5) in a 1-m-radius sphere around the bird, mode of searching or prey attack (including associated postures, such as hanging), substrate (including specific characteristics, such as leaf size and type), and perch type. Because dead-leaf searching species sought prey primarily hidden inside substrates, it was often impossible to distinguish between searching maneuvers and prey captures. I therefore recorded all unambiguous visual searches and included these in analyses of substrate use. Otherwise, my categorization of behaviors closely followed that of Remsen and Robinson (1990). I also noted associated bird species and any interactions among flock members.

I assessed the arthropod diet of each species directly to determine degree of prey selectivity and resource partitioning among dead-leaf specialists. Birds were collected for stomach analysis using mist-nets and shotguns, primarily at the Pando study site and on the Río Shesha, depto. Ucayali, Peru. The Río Shesha site was in hilly lowland rainforest with an avifauna typical of western Amazonia and similar to that of both Pando and Tambopata (LSUMNS unpubl. data). These samples were supplemented with a few birds taken elsewhere in eastern Peru and northern Bolivia (LSUMNS Stomach Contents Collection). All stomach samples were preserved directly in 70% ethanol as soon as possible after collection.

Stomach contents were sorted and identified to lowest taxonomic category possible under a 6X–25X dissecting microscope. Minimum number of prey items in each category was determined from diagnostic fragments, such as mouthparts, heads and wings. Identification of arthropod fragments was facilitated by dissecting voucher specimens collected at the study sites and by illustrations in Ralph et al. (1985), Moreby (1987), and Chapman and Rosenberg (1991). Prey sizes were estimated by measuring characteristic parts with an optical micrometer. Fragment size was then converted to prey length using regression equations in Calver and Wooller (1982), Diaz and Diaz (1990), or those determined in the present study. Each individual stomach was considered as a sample, and the diet of each species was determined by averaging the proportions of each prey category across individuals (i.e., samples were not pooled).

**Resource subdivision and partitioning.**—To assess relative specialization along finer axes of foraging height, substrate type, dead-leaf size, diet composition, and prey size, I calculated niche breadth as  $B = 1/\sum p_i^2$ , where  $p_i$  is the proportion of category  $i$  in the sample (Levins 1968). Each niche measure was divided into 10 categories to allow for comparisons of breadth across variables. Overlaps between each species pair were then calculated for each variable as  $O_a = \sum P_{ia}P_{ja}\sqrt{(\sum P_{ia}^2)(\sum P_{ja}^2)}$ , where  $P_{ia}$  and  $P_{ja}$  are the proportional uses of resource state “ $a$ ” by species  $i$  and  $j$  respectively (Pianka 1974, May 1975). In addition, I calculated two combined measures of overlap: foraging space, equal to the product of  $O_{\text{height}}$  and  $O_{\text{substrate}}$ ; and diet, equal to the product of  $O_{\text{prey-type}}$  and  $O_{\text{prey-size}}$ . I used “product-alpha” (Cody 1974) in these cases because the measures being combined represented relatively independent niche parameters.

Differences between species were tested for continuous measures (foraging height, leaf size, prey size) using the Kolmogorov-Smirnoff test and for categorical measures (substrate, prey type) using the G-test. Details of pairwise comparisons may be found in Rosenberg (1990b).

**Resource availability.**—Numbers of suspended dead leaves within 10 m of the ground were assessed on randomly placed 10-m line transects perpendicular to existing trails, as described in

TABLE 1  
CHARACTERISTICS OF 16 DEAD-LEAF FORAGING BIRD SPECIES IN SOUTHWESTERN AMAZONIA.  
HABITAT AND FLOCK TYPES ARE LISTED IN ORDER OF IMPORTANCE

Species	Code	Body weight <sup>1</sup>	Habitat <sup>2</sup>	Flock type <sup>3</sup>	% Dead leaves <sup>4</sup>	Number of obs.
<b>CAPITONIDAE</b>						
<i>Capito niger</i>	CN	62.5	U, L	C, SC	73	121 <sup>5</sup>
<i>Eubucco richardsoni</i>	ER	31.8	L	C, SC	97	136 <sup>5</sup>
<b>DENDROCOLAPTIDAE</b>						
<i>Xiphorhynchus guttatus</i>	XG	57.8	L, U	U, SC, C	63	331
<b>FURNARIIDAE</b>						
<i>Cranioleuca gutturalata</i>	CG	14.9	L	SC, U	70	96
<i>Philydor erythrocerus</i>	PE	26.3	U	SC, U	80	122
<i>Philydor ruficaudatus</i>	PR	30.1	L	SC, C	92	36
<i>Automolus rufigularis</i>	AR	36.5	L	U, SC	100	107
<i>Automolus ochrolaemus</i>	AO	33.8	L	U	94	236
<i>Automolus melanopezus</i>	AM	30.7	L	U	97	283
<i>Automolus infuscatus</i>	AI	38.8	U, L	U	88	201
<i>Hyloctistes subulatus</i>	HS	27.1	U, L	SC, U	85	20
<b>FORMICARIIDAE</b>						
<i>Pygiptila stellaris</i>	PS	24.1	L, U	C, SC, U	58	338
<i>Myrmotherula leucophthalma</i>	ML	9.3	L, U	U	99	1,137
<i>Myrmotherula haematonota</i>	MH	8.7	U	U	94	81
<i>Myrmotherula ornata</i>	MO	9.5	L	U	98	538
<b>TROGLODYTIIDAE</b>						
<i>Thryothorus genibarbis</i>	TG	18.5	L	U	95	116

<sup>1</sup> Mean of 5 male and 5 female specimens (grams).

<sup>2</sup> U = Upland forest; L = Low-lying forest.

<sup>3</sup> Type of mixed-species foraging flock: C = Canopy; SC = Subcanopy; U = Understory.

<sup>4</sup> Percent of foraging observations at dead-leaf substrates.

<sup>5</sup> Includes only insectivorous foraging.

Rosenberg (1990a). I established 10 transects in each habitat at each site; leaves were censused at Pando in July 1986 and at Tambopata in May and July 1987 and in July and October 1988. During each census, I counted all dead leaves and clusters in a 1-m wide strip and recorded the distribution of leaf sizes (to the nearest 1 cm) and types, especially palms, bamboo, and *Cecropia* leaves. I also measured the accumulation, persistence, and turnover of individual leaves in each habitat at Tambopata, as described by Rosenberg (1990a).

The arthropod fauna of aerial litter was sampled by placing individual dead leaves in zip-lock plastic bags and spraying them with insecticide; arthropods exited the leaves and were easily separable. All arthropods were identified to the lowest taxonomic level possible, measured to the nearest 1 mm, and preserved in 70% ethanol. Characteristics of each leaf (e.g., size, type) were also recorded at the time of collection. I selected leaves in two ways. At Pando and at Tambopata in 1987, samples consisted of the first 30–50 dead leaves encountered 1–2 m above ground, along transects from randomly determined starting points along a trail. Some leaves proved impossible to collect without disturbing their arthropod inhabitants; therefore, these samples may be somewhat biased towards more exposed leaves. At Tambopata in 1988, I established 30 1-m<sup>3</sup> plots, 1–2 m above ground in low-lying forest. Within each plot I searched for arthropods on every substrate surface, including all live and dead leaves. In this way, I determined arthropod density on live vs. dead leaves, in addition to number per leaf. Arthropods on live foliage were also assessed by visually searching leaf surfaces in areas adjacent to the dead-leaf samples described above.

## RESULTS

**Dead-leaf foraging guild.**—Sixteen bird species were found to feed most frequently at suspended dead leaves at either the Pando or Tambopata sites (Table 1). Ten species occurred at both sites and showed little or no variation in degree of specialization between areas. Fifteen of these 16 species were regular members of mixed-species feeding flocks, based on censuses of

92 flocks at Tambopata (82 in low-lying forest, 10 in upland; Rosenberg unpubl. data). Two barbets (Capitonidae) were regular members of canopy feeding flocks, searching for both insects and fruit. *Eubucco richardsoni* was common only in low-lying forest at Tambopata (33% of canopy flocks) and was very rare at Pando; virtually all of its insectivorous foraging was at dead leaves. *Capito niger* occurred in most forest types at both sites. It was a more generalized forager, searching branch and trunk surfaces in addition to dead leaves. One woodcreeper, *Xiphorhynchus guttatus*, foraged at dead leaves more than on any other substrate and was often the most conspicuous dead-leaf forager in any particular mixed-species flock. It occurred widely in most forest types, joining flocks in the canopy or understory (39% of all flocks).

As noted by Remsen and Parker (1984), most dead-leaf specialists belong to the families Furnariidae or Formicariidae (Table 1). Seventy-six percent of understory flocks in both forest types contained at least one species of *Automolus* foliage-gleaner. *Automolus rufipileatus* was restricted to river-edge forest at Tambopata, usually with extensive thickets of bamboo in the understory. *Automolus ochrolaemus* and *A. melanopezus* occurred in low-lying forest with bamboo at both sites; *A. ochrolaemus* was more widespread at Tambopata in dense, low-lying forest away from bamboo (40% of flocks). *Automolus infuscatus* was the common species in upland forest at both sites (55% of flocks) and also in more open areas of low-lying forest at Tambopata far from bamboo (22% of flocks). Of the five species of *Philydor* foliage-gleaners in this region, only *P. erythrocercus* and *P. ruficaudatus* are apparently dead-leaf specialists. *Philydor erythrocercus* was fairly common in upland forest at both sites (30% of flocks); it was often the only specialist in canopy flocks. *Philydor ruficaudatus* was rare, occurring only in a few canopy flocks in low-lying forest at Tambopata. The other *Philydor* species (*erythropterus*, *pyrrhodes*, and *rufus*) may use dead leaves regularly, but concentrate their foraging more on live foliage (especially palms). *Hyloctistes subulatus* is only tentatively listed as a dead-leaf specialist because of my small sample of observations. It was uncommon in upland forest at Pando and was inexplicably rare at Tambopata during the study period. Its inclusion is supported, however, by observations of this species in lowland forest in Costa Rica, where 70% of 37 foraging attempts were at dead leaves (pers. obs.). *Cranioleuca gutturalis* foraged in dense parts of the subcanopy in low-lying forest at Tambopata, travelling with either understory or low canopy flocks (16% of flocks). It foraged along branches and vines in addition to searching trapped dead leaves. An additional furnariid, *Thripophaga fusciceps*, was listed as a specialist by Remsen and Parker (1984); although it is recorded from Tambopata, I did not observe it.

Of the antbirds, *Pygiptila stellaris* was the only canopy-flocking species that used dead leaves to a large extent. Although only 58% of its foraging was at dead leaves, it is included here because when feeding at these leaves this species employed many of the same behaviors (see below) exhibited by other specialists. Individual *P. stellaris* were observed to switch between bouts of dead-leaf foraging and searching live foliage, and this was the only species for which dead-leaf foraging appeared to be height-dependent; they searched dead leaves significantly more when in understory or sub-canopy flocks (i.e.,  $\leq 10$  m) than in the upper canopy ( $X^2 = 20.4$ ;  $P < 0.001$ ).

Three small antwrens are extreme specialists in this region (94%–99% of foraging; Table 1). *Myrmotherula leucophthalma* was the most widespread, occurring in most (73%) forest understory flocks at Tambopata, but restricted to streamside bamboo and disturbed forest at Pando. In upland forest at Pando, this species was replaced by *M. haematonota* (Parker and Remsen 1987). *Myrmotherula ornata* was common in the vicinity of bamboo thickets at Tambopata and often occurred in the same mixed flocks as *M. leucophthalma* in this habitat (41% of flocks). The remaining specialist is a wren, *Thryothorus genibarbis*, which lived primarily in bamboo thickets at both sites, as well as in other disturbed and river-edge forest. This species foraged in solitary pairs or family groups and only occasionally joined understory flocks that passed through their territories.

Thus, each forest type supported a distinct assemblage of dead-leaving birds. In upland forest, understory flocks contained two species, and one to three species occurred in the canopy. In low-lying forest, especially with bamboo, many more species were present, with up to five species in understory flocks and five or six in some canopy flocks. When, on occasion, an understory flock temporarily joins with a sub-canopy flock, as many as nine dead-leaving species may forage in close proximity. The importance of bamboo to certain guild members will be discussed further below. Note also that the most specialized members of the guild (i.e., >75%) were nearly all understory species; canopy foragers (except *Philydor* spp.) were either partly frugivorous or regularly searched live foliage, branches or vines.

The 16 species included in this study represent roughly 20% of the 84 insectivorous species

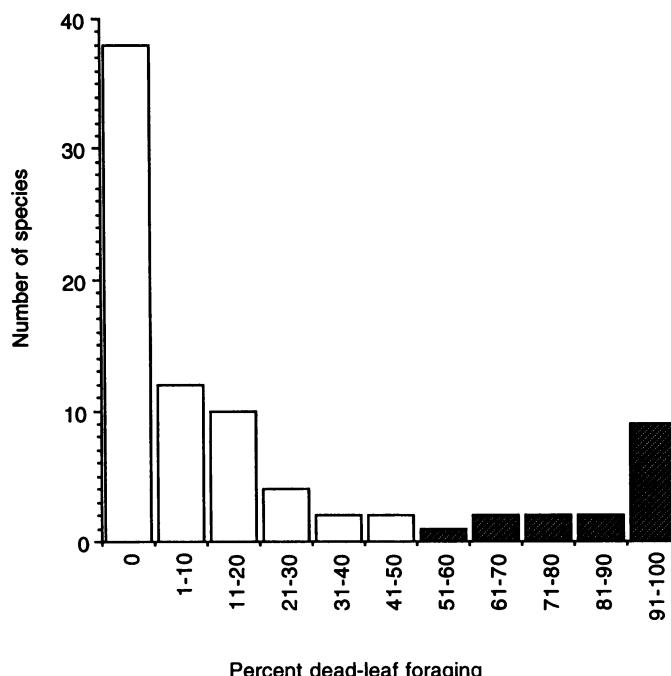


FIG. 1. Distribution of dead-leaf foraging among 84 insectivorous bird species in southwestern Amazonia. Based on 6962 observations at Pando, Bolivia and Tambopata, Peru. Shaded species are specialists considered in this study.

for which I collected foraging data (Fig. 1). An additional 38 species never were observed to forage on dead-leaf substrates. The remaining insectivorous birds at these forest sites inspected dead leaves opportunistically, but this usually accounted for <20% of their foraging (Fig. 1). A few species, however, regularly included dead leaves in their repertoires, although these substrates were not specifically sought out and the birds rarely if ever used specialized behaviors to inspect leaves or extract prey (see below). Remsen and Parker (1984) listed several species as "Regular Users" of dead leaves (25%–75% of observations). A few of these I have placed in the specialist guild above, and my observations suggest several others also are regular users; *Myrmotherula hauxwelli* (50% of 70 observations), *M. iheringi* (47% of 219 obs.), *Ancistrops strigilatus* (32% of 134 obs.), *Hypocnemis cantator* (31% of 54 obs.), *Philydor pyrrhodes* (29% of 41 obs.), *Microrhopias quixensis* (26% of 34 obs.), and *Dendrexetastes rufigula* (23% of 52 obs.). One additional regular user listed by Remsen and Parker (1984) was the ant-tanager *Habia rubica*. This species proved to be an extreme generalist, using dead-leaf substrates in 29% of 78 observations. Finally, my limited observations of a few other species included bouts of systematic dead-leaf searching; these were *Philydor rufus*, *Myrmeciza hyperythra*, *Thryothorus leucotis*, *Campylorhynchus turdinus*, *Paroaria gularis*, *Icterus icterus*, *Cacicus cela*, and *Psarocolius decumanus*. The extent to which these species may be specialized remains to be quantified.

**Species-specific behaviors.**—Dead-leaf specialists typically moved directly from leaf to leaf, inspecting them for hidden arthropod prey and ignoring intervening areas of live foliage or other substrates. Because dead leaves were often suspended in difficult to reach places or on flimsy substrates, the birds often employed acrobatic postures or behaviors to inspect them. Extending the body or neck (reaching) or hanging with legs extended was observed frequently in all species (Table 2). The "hanging" category includes clinging directly to the dead leaf and (especially in *E. richardsoni* and *Philydor* spp.) the completely vertical suspension of the body to reach leaves directly below a perch. These behaviors were not unique to dead-leaf foraging species, however; reaching was commonly observed in other arboreal foliage-gleaning species, and hanging is a characteristic behavior in certain genera (e.g., *Xenops*, *Terenura*, *Hylophilus*; pers. observ.).

In general, what separated guild members from other birds that occasionally inspected dead leaves was their tendency to manipulate these substrates physically with their bills or feet. All species studied picked at dead leaves with their bills on at least 50% of their foraging attempts

TABLE 2  
PERCENT USE OF UNUSUAL POSTURES AND BEHAVIORS ASSOCIATED WITH DEAD-LEAF FORAGING IN  
16 AMAZONIAN BIRDS

Species (N)	Reach/ lean	Hang	Use bill (pick)	Pull	Hold	Tear	Thrash
<i>Capito niger</i> (88)	44	17	81	17	11	9	0
<i>Eubucco richardsoni</i> (124)	37	52	81	11	7	13	0
<i>Xiphorhynchus guttatus</i> (200)	8	21	83	0	0	2	20
<i>Cranioleuca gutturalis</i> (62)	13	42	57	0	0	0	0
<i>Philydor erythrocercus</i> (104)	18	48	68	2	3	0	1
<i>P. ruficaudatus</i> (28)	25	50	89	0	0	0	0
<i>Automolus rufipileatus</i> (94)	16	22	72	3	3	4	6
<i>A. ochrolaemus</i> (230)	16	30	56	1	1	1	4
<i>A. melanopezus</i> (271)	22	27	61	2	2	2	6
<i>A. infuscatus</i> (208)	24	15	56	1	2	1	4
<i>Hyloctistes subulatus</i> (19)	0	68	74	0	0	0	5
<i>Pygiptila stellaris</i> (191)	27	10	59	2	0	1	5
<i>Myrmotherula leucophthalma</i> (741)	34	31	58	0	0	0	1
<i>M. haematonota</i> (78)	23	44	68	0	0	0	0
<i>M. ornata</i> (512)	26	21	52	0	0	0	1
<i>Thryothorus genibarbis</i> (94)	34	15	65	0	0	0	6

(Table 2). This behavior was often associated with cocking the head to listen, or peering inside the leaf, and served to jostle or flush otherwise immobile and hidden prey. Non-specialists visually inspected dead leaves but rarely disturbed the leaves to facilitate prey detection. This fundamental difference in behavior was confirmed with close observations of captive birds (Rosenberg 1993).

In addition to simply picking at a leaf, some species exhibited more complex behaviors to aid in prey capture. One such tactic was to pull a suspended leaf closer to the bird with the bill and (usually) grab or hold the leaf with the foot. This technique was used most frequently by the barbets and was observed consistently in nearly all the larger furnariid species (Table 2). Typically, a leaf was held next to a branch with the foot, and the prey was extracted with the bill from beneath the feet. A variation was seen in *P. erythrocercus*, in which the birds hung acrobatically with one foot, reached out and grabbed a leaf (usually undehisced) with the other foot and pulled it to the face to peer inside or extract prey, much in the manner of a parrot. The antbirds, as well as *Thryothorus genibarbis* and *Cranioleuca gutturalis*, did not exhibit these additional behaviors. In particular, no antbird was seen to use its feet to manipulate substrates or prey, in the wild or during feeding experiments (Rosenberg 1993). *Pygiptila stellaris* occasionally tugged on a leaf with its bill, and the *Myrmotherula* antwrens rarely used the bill to bite down on curled leaves to test for hidden prey.

Another behavior distinguishing the barbets and large furnariids (*Automolus*) from the other species was their tendency to tear apart large leaves in search of prey. As pointed out by Remsen and Parker (1984), this behavior often destroys the leaf as a future hiding place for arthropods. Another "destructive" searching technique, used most frequently by *Xiphorhynchus guttatus*, was to thrash and toss leaves from clusters, often knocking them to the ground. Overall, the behaviors of *Myrmotherula* spp., *Cranioleuca gutturalis*, and *Philydor* spp. were least destructive to the leaves and allowed them to serve as potentially renewable resource patches (see below).

**Habitat associations.**—Birds already specialized on dead-leaf substrates apparently subdivide this resource in a number of ways. As noted above (Table 1), many species were restricted to only one major habitat (forest type), and different combinations of species coexisted in each forest. Segregation by habitat was most evident among congeners. For example, *Philydor*, *Automolus*, and *Myrmotherula* all showed species replacements between upland and lowland forests at one or both sites.

The presence of bamboo has been recognized as an important habitat component for birds in southwestern Amazonia (Parker 1982, Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Kratter 1993). On my study sites, *A. melanopezus*, *A. rufipileatus*, *M. ornata*, and *T. genibarbis* were absent in forests without at least some bamboo, although segregation among congeners was far from absolute. For example, *M. ornata* joined some flocks containing *M. leucophthalma* at Tambopata. *A. melanopezus* and *A. ochrolaemus* occasionally occurred in the same flocks at both

sites, and *A. rufipileatus* occurred with either of these species at Tambopata. However, even in low forest, *A. infuscatus* avoided areas with any bamboo and therefore rarely overlapped with other *Automolus* species.

Except for a few well-defined dense thickets, bamboo was distributed patchily throughout the low-lying forest at Tambopata. Consequently, flocks containing dead-leaving species encountered a gradient of bamboo densities, making it difficult to assign specific observations as either "bamboo" or "nonbamboo." Therefore, I consider only two habitat types, upland and low-lying forest, in the following comparisons.

I tested for spatial associations among dead-leaving species in 92 mixed-species flocks at Tambopata using Cramer's V (Pielou 1977:201); this is essentially a correlation coefficient between two species, based on their pattern of co-occurrence in individual flocks. No significant negative associations existed between any species pair in either forest type (Appendix). The strongest positive associations (only two significant) were among species sharing an affinity for bamboo (listed above) and those foraging at similar heights in the canopy (e.g., *Eubucco richardsoni* with *Capito niger* and *Philydor* spp.; *Xiphorhynchus guttatus* with *Pygiptila stellaris*). In fact, overlap in foraging height was the only variable significantly (although weakly) correlated with this measure of association ( $r = 0.284$ ;  $P < 0.01$ ). The strongest negative associations (none significant) were between canopy and low understory species, which tended to travel in separate flocks, and between *A. infuscatus* and the above-listed bamboo species.

**Foraging height and leaf size.**—Within each habitat, most species differed significantly from each other in either their foraging height distributions or the average sizes of leaves searched (Appendix; for details of pairwise comparisons, see Rosenberg 1990b). Species overlapped more (i.e., were more densely packed) in low-lying forest than in upland forest (Fig. 2). The additional species in low-lying forest were primarily understory foragers, and more guild members searched larger leaves in low-lying forest than in upland. Among the understory species in both habitats, size of leaves searched was highly correlated with body size (weight) ( $r = 0.897$ ;  $P < 0.001$ ), but this relationship disappeared if canopy birds were included.

The breadths of foraging heights and leaf sizes used were similar among most species (Table 3). *Myrmotherula haematonota* exhibited the most restricted height range, and *X. guttatus* the broadest. On average, species in upland forest used a narrower range of heights than species in low forest. *Pygiptila stellaris* and *C. gutturalis* showed the greatest diversity of leaf-sizes used, and *T. genibarbis* and *X. guttatus* showed the lowest.

**Foraging site.**—Because dead leaves could become trapped above ground in a variety of situations in the forest, guild members had the opportunity to concentrate their foraging efforts in particular microhabitats (Table 4). Barbets, for example, along with *Philydor erythrocerus*, foraged more than other species on bare twigs and branches; these species also consequently were seen in more open, exposed areas, as reflected by their lower average foliage density measures than all other species. *Xiphorhynchus guttatus* searched for dead leaves relatively frequently along trunks and on large canopy palm fronds. Many species foraged in dense vine-tangles, where leaves often gathered in large clusters. These areas were particularly important to *C. gutturalis* and *T. genibarbis*, and probably *P. ruficaudatus* and *H. subulatus*. *Myrmotherula haematonota* at Pando, and *M. leucophthalma* in upland forest at Tambopata, fed frequently in understory palm vegetation (especially *Geonoma* spp.). Although six species commonly occurred in bamboo habitats, only *A. rufipileatus* and *M. ornata* foraged often within bamboo foliage.

Most dead-leaving species showed a tendency to perch directly on the leaves being searched (Table 4), another behavior rarely seen in other species that only occasionally inspected dead leaves. This was most evident in *X. guttatus*, which hung on dead palm fronds and clung to large *Cecropia* leaves, and in *M. haematonota*, which routinely clung to the tips of understory palm leaflets. Other species, such as *C. gutturalis*, *C. niger*, and *P. erythrocerus*, most often inspected leaves from adjacent perches.

**Substrate types.**—Perhaps the most important way in which guild members differed was in their use of various types of dead leaves and other substrates (Fig. 3). Based on 10 substrate categories (including live foliage and branches), nearly every species pair in both habitats differed significantly in substrate use (Appendix). Among the canopy species, *C. niger* and *X. guttatus* often inspected large, suspended *Cecropia* leaves. *Xiphorhynchus guttatus* also inspected large dead palm fronds and clusters of leaves, which were not exploited by *C. niger*. *Eubucco richardsoni* and *P. erythrocerus* rarely used these distinctive leaf-types or clusters but instead concentrated their foraging at relatively small (10–12 cm) leaves that were often undehisced at the tips of dead branches (48% and 30% respectively). In my small sample of observations for *P. ruficaudatus*, 39% of the leaves searched also were undehisced on branch-tips. This contrasts

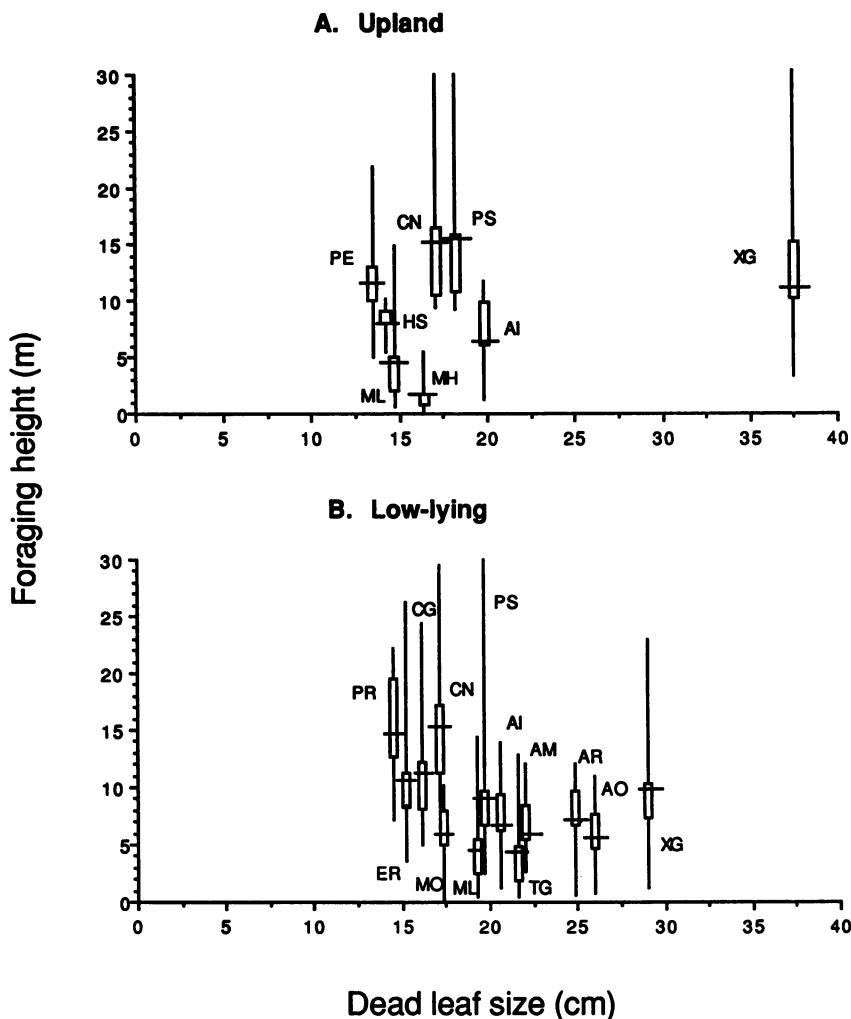


FIG. 2. Foraging heights and average leaf sizes used by dead-leaf foraging birds in Upland (A) and Low-lying (B) Amazonian forest. Horizontal line = mean height; vertical bar = modal 50% of observations; vertical line = height range. Bird species codes from Table 1.

with nearly every other species, which searched mostly leaves that had fallen and lodged on branches or vines.

In the understory, all *Automolus* spp. exploited large and distinctive leaf types, such as *Cecropia* and palms, as well as dead-leaf clusters (Fig. 3). Among the smaller antwrens, *M. leucophthalma* in upland forest at Tambopata, and *M. haematonota* in upland forest at Pando, both fed frequently at understory palm leaflets (e.g., *Geonoma* spp.). In low-lying forest at Tambopata, *M. ornata* differed greatly from *M. leucophthalma* in its heavy use of dead bamboo leaves. At Pando, however, where *leucophthalma* was the only *Myrmotherula* in bamboo, it often fed in dead bamboo foliage. *Thryothorus genibarbis* at both sites fed most often at dead bamboo and *Cecropia* leaves and in large clusters.

Diversity of substrates used ranged from 2.21 (*E. richardsoni*) to 6.44 (*T. genibarbis*), out of a possible 10.00 (Table 3). Both *A. infuscatus* and *M. leucophthalma* used a narrower range of foraging substrates in upland forest than in low-lying forest, but the average breadth for all upland species combined was only slightly less than for low-lying forest species. Substrate diversity was not related to foraging height, leaf size, or body size in these birds.

**Substrate availability.**—Suspended dead leaves were abundant in all forest habitats at each

TABLE 3  
FORAGING AND DIETARY DIVERSITY (NICHE BREADTH) IN 16 DEAD-LEAF SEARCHING BIRDS. NICHE BREADTH =  $1/\sum P_i A^2$  (SEE TEXT); EACH MEASURE BASED ON 10 CATEGORIES

Species	Height	Leaf size	Substrate	Prey type	Prey size
<i>Capito niger</i>	4.92	5.52	6.28	4.64	3.57
<i>Eubucco richardsoni</i>	4.09	4.93	2.21	4.20	3.76
<i>Xiphorhynchus guttatus</i>	5.11	4.48	5.52	3.80	4.83
<i>Cranioleuca gutturata</i>	4.85	6.74	5.74	3.18	1.97
<i>Philydor erythrocercus</i>	3.46	5.05	3.43	4.35	5.08
<i>P. ruficaudatus</i>	2.99	6.22	4.00	4.45	4.31
<i>Automolus rufipileatus</i>	4.78	5.39	5.44	5.98	5.02
<i>A. ochrolaemus</i>	4.80	5.66	6.09	3.65	6.17
<i>A. melanopezus</i>	4.16	5.29	4.64	3.32	5.00
<i>A. infuscatus</i> (upland)	4.62	5.39	3.74	4.70	2.96
<i>A. infuscatus</i> (low-lying)	4.84	5.53	5.16	—	—
<i>Hyloctistes subulatus</i>	2.37	—	4.76	3.37	5.77
<i>Pygiptila stellaris</i>	4.04	7.45	4.08	4.39	5.97
<i>Myrmotherula leucophthalma</i> (upland)	4.89	6.19	3.72	—	—
<i>M. leucophthalma</i> (low-lying)	4.16	5.53	4.62	—	—
<i>M. leucophthalma</i> (Pando)	3.12	—	4.47	4.08	4.39
<i>M. haematonota</i>	2.22	4.58	3.85	2.60	3.59
<i>M. ornata</i>	4.80	4.91	4.98	4.64	2.57
<i>Thryothorus genibarbis</i>	4.36	4.30	6.44	5.26	3.52
Upland (ave.)	3.85	5.52	4.42	3.98	4.49
Low-lying (ave.)	4.32	5.53	4.98	4.30	4.66

site. Rosenberg (1990a) reported a seasonal change in leaf abundance in two of three habitats at Tambopata in 1987. Repeated sampling in 1988 revealed that local variation among transects was greater than seasonal changes within a habitat (Rosenberg 1990b). Greatest concentrations of dead leaves were in the vicinity of tree-fall gaps or dense vine-tangles; also, local variation in leaf drop from particular tree species (e.g., *Cecropia*) contributed greatly to changes in leaf abundance.

At Tambopata, the density of dead leaves was consistently lower in upland forest ( $x = 3.9/m^3$ ) than in low-lying forest with ( $5.1/m^3$ ) or without ( $4.7/m^3$ ) bamboo. At Pando, leaf density was higher, averaging  $6.2/m^3$  in upland forest and  $6.7/m^3$  in bamboo. In all areas, dead leaves

TABLE 4  
PERCENT USE OF PERCH AND FORAGING SITES IN 16 DEAD-LEAF SEARCHING BIRDS. FD = FOLIAGE DENSITY IN A 1-M RADIUS SPHERE AROUND BIRD (SCALE, 1-5)

Species (N)	On leaf	Vine tangle	Live branch	Dead branch	Trunk	Palm	Bamboo	FD (ave.)
<i>Capito niger</i> (47)	9	10	47	32	2	0	0	2.2
<i>Eubucco richardsoni</i> (97)	23	13	20	34	0	0	0	2.2
<i>Xiphorhynchus guttatus</i> (175)	42	13	10	0	21	14	0	3.0
<i>Cranioleuca gutturata</i> (115)	3	52	23	6	2	4	0	3.4
<i>Philydor erythrocercus</i> (85)	11	20	26	32	5	7	0	2.1
<i>P. ruficaudatus</i> (33)	21	55	6	18	0	0	0	3.3
<i>Automolus rufipileatus</i> (99)	23	28	22	1	0	2	36	3.6
<i>A. ochrolaemus</i> (266)	13	36	28	6	1	5	9	3.3
<i>A. melanopezus</i> (261)	20	38	26	3	0	3	10	3.4
<i>A. infuscatus</i> (210)	14	34	36	4	0	6	0	3.1
<i>Hyloctistes subulatus</i> (20)	30	55	0	15	0	0	0	3.3
<i>Pygiptila stellaris</i> (155)	14	29	43	6	0	5	4	3.3
<i>Myrmotherula leucophthalma</i> (upland) (154)	22	17	21	16	0	30	0	2.8
<i>M. leucophthalma</i> (low) (572)	20	31	30	7	0	8	4	3.0
<i>M. haematonota</i> (71)	39	1	18	8	0	38	0	2.7
<i>M. ornata</i> (494)	10	32	15	6	0	4	38	3.0
<i>Thryothorus genibarbis</i> (77)	25	53	0	0	0	0	0	3.8

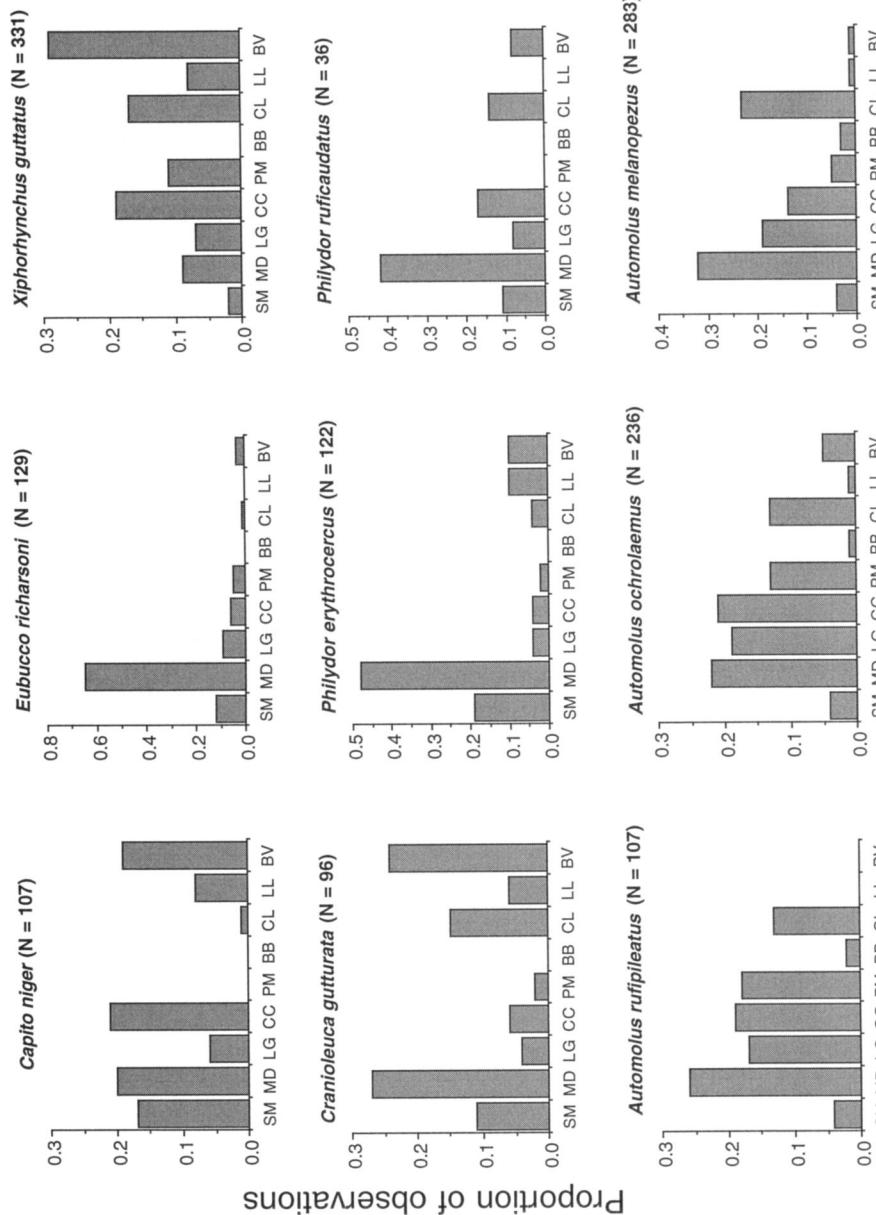


FIG. 3. Use of substrate types by dead-leaf foraging birds in sw Amazonia. SM, MD, LG = small (3–8 cm), medium (10–15 cm), and large ( $\geq 20$  cm) curled dead leaves; CC = dead *Cecropia* leaves; PM = dead palm fronds; BB = dead bamboo leaves; CL = dead leaf clusters; LL = live leaves; BV = branches and vine stems.

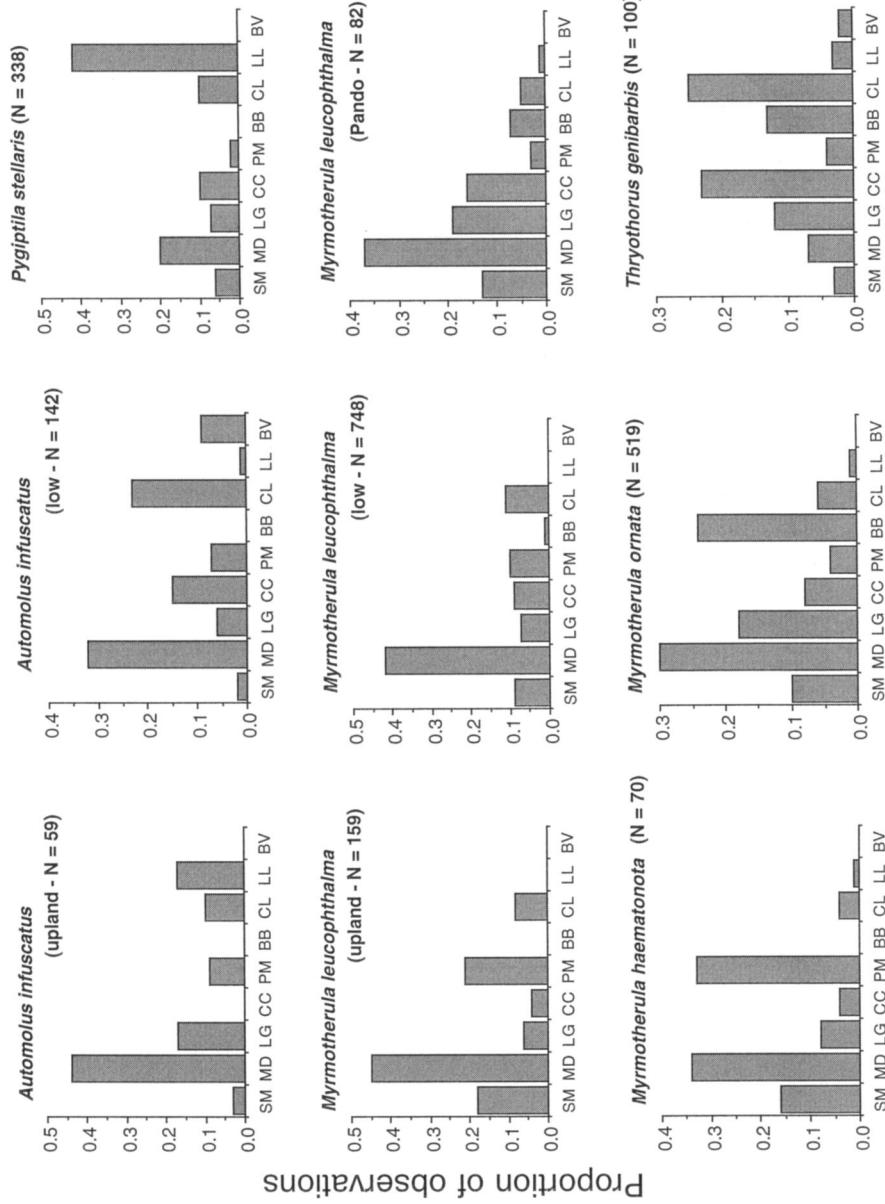


FIG. 3. Continued.

were concentrated in the first 3 m above the ground (Rosenberg 1990a). At Tambopata, overall height distribution of dead leaves was similar in all habitats, but with a tendency for bamboo sites to have more dead leaves at mid-levels (3–5 m) than did upland forest. At Pando, this was more pronounced, with a much greater proportion of leaves above 3 m in bamboo (51%) than in upland forest (25%).

Distribution of dead-leaf sizes and types differed among habitats, with each habitat offering particular distinctive leaf-types, such as palms, bamboo, or *Cecropia* leaves (Fig. 4). In upland forest at Tambopata, understory palm leaflets (mostly *Geonoma* spp.) made up 39% of the available dead leaves below 2 m. Above that height, small or medium-sized curled or entire leaves were most abundant. In low-lying forest, 44% of the leaves above 5 m were large palm fronds (*Iriartea* spp., *Socratea* spp.), whereas at lower levels, curled leaves ≤ 15 cm predominated. In bamboo thickets, dead bamboo leaves were most abundant at all levels, and *Cecropia* leaves made up 13% of the available dead leaves above 5 m. *Cecropia* leaves were patchily distributed, mostly in the vicinity of light-gaps and close to rivers (up to 8 leaves/m<sup>3</sup>).

At Tambopata, overall average dead-leaf size ranged from 14.5 cm in upland forest to 17.3 cm in low forest without bamboo. In each habitat, average leaf size was highest above 5 m (Fig. 4). At Pando, dead leaves averaged smaller in both habitats (11.7 cm in upland; 11.3 cm in bamboo), primarily because of the scarcity of large palm or *Cecropia* leaves. In upland forest, 16% of the leaves below 2 m were palms (mostly *Geonoma* spp.). Bamboo at Pando was structurally quite different from that at Tambopata; leaves were shorter (15 cm vs. 18–20 cm) and thinner (< 1 cm), and formed dense mats after dying, rather than lodging and curling individually. Because of difficulty enumerating dead bamboo leaves at Pando, leaf densities underestimated the total number of dead-leaf substrates available in this habitat.

Considering only nonentire leaves ≥ 8 cm as a closer measure of leaf availability to birds, differences between habitats were more marked. Upland forest supported nearly 50% fewer suitable leaves in 1987 than did bamboo thickets (2.6/m<sup>3</sup> versus 3.8/m<sup>3</sup>), with low forest being intermediate (3.4/m<sup>3</sup>). In addition, the proportion of total dead leaves considered suitable was greater in bamboo (84%) than in upland (69%) or low forest (72%).

**Diet.**—Diets of nearly all species were qualitatively similar, differing only in the proportions of major prey taxa (Fig. 5). Because of low variability among individuals, samples of five to six stomachs were adequate to represent the diets of most species (see Rosenberg and Cooper 1990). In six species, samples of three or more stomachs from each collecting locality allowed a geographic comparison in diets. In no case were there significant differences in prey types eaten between sites (G-tests; *P*'s > 0.27). Therefore, I believe that pooling samples from several Amazonian localities is justified.

The barbets were largely frugivorous; on average, 37% of the food items in stomachs of *Eubucco richardsoni* and 18% of those in *Capito niger* were arthropods. These percentages support the estimates of frugivory found for these genera in a broader diet survey of barbets and other tropical bird families (Remsen et al. 1993). Those arthropods I identified in barbet stomachs indicate that the animal portion of these species' diets is similar to those of other dead-leaf foraging species (Fig. 5). In all remaining species except *Cranioleuca gutturalis*, most of the diet (64%–94%) consisted of Orthoptera (including roaches), beetles, and spiders. The large woodcreeper, *X. guttatus*, ate more beetles and fewer orthopterans than most other species, whereas in *A. melanopezus*, *H. subulatus*, and *M. haematonota*, 50% or more of the prey consumed were katydids or crickets. In general, smaller species (e.g., *Myrmotherula* spp.) ate more roaches and spiders than did larger species (e.g., *Automolus* spp.). Species feeding in bamboo tended to eat more Heteroptera (mostly Pentatomidae) than species restricted to upland forest. Remains of vertebrate prey were found in eight species, including the relatively small-billed *T. genibarbis*. All identifiable bones were of iguanid lizards (probably *Anolis* spp.), except for two tree-frogs eaten by *A. melanopezus* and *A. rufipileatus*. Finally, the diet of *Cranioleuca gutturalis* was notably different from all other species studied, consisting mostly of small Homopterans (leafhoppers) and ants. Unfortunately, my small sample of stomachs was from northeastern Peru; therefore, the uniqueness of this species' diet must be considered tentative.

Dietary diversity was lowest in *M. haematonota* (2.92), which ate the highest proportion of orthoptera, and *C. gutturalis* (3.18) and was highest in *A. rufipileatus* (5.98) and *X. guttatus* (5.72) (Table 3). All other species ranged from 3.32 to 4.70 (out of a possible 10.00). On average, species in upland forest exhibited a narrower dietary breadth than those in low forest. This measure was otherwise not related to a species' body or bill size, taxonomic affinity, foraging height, substrate diversity, or number of stomachs examined.

Average size of prey eaten was positively correlated with bill size in these bird species (Fig.

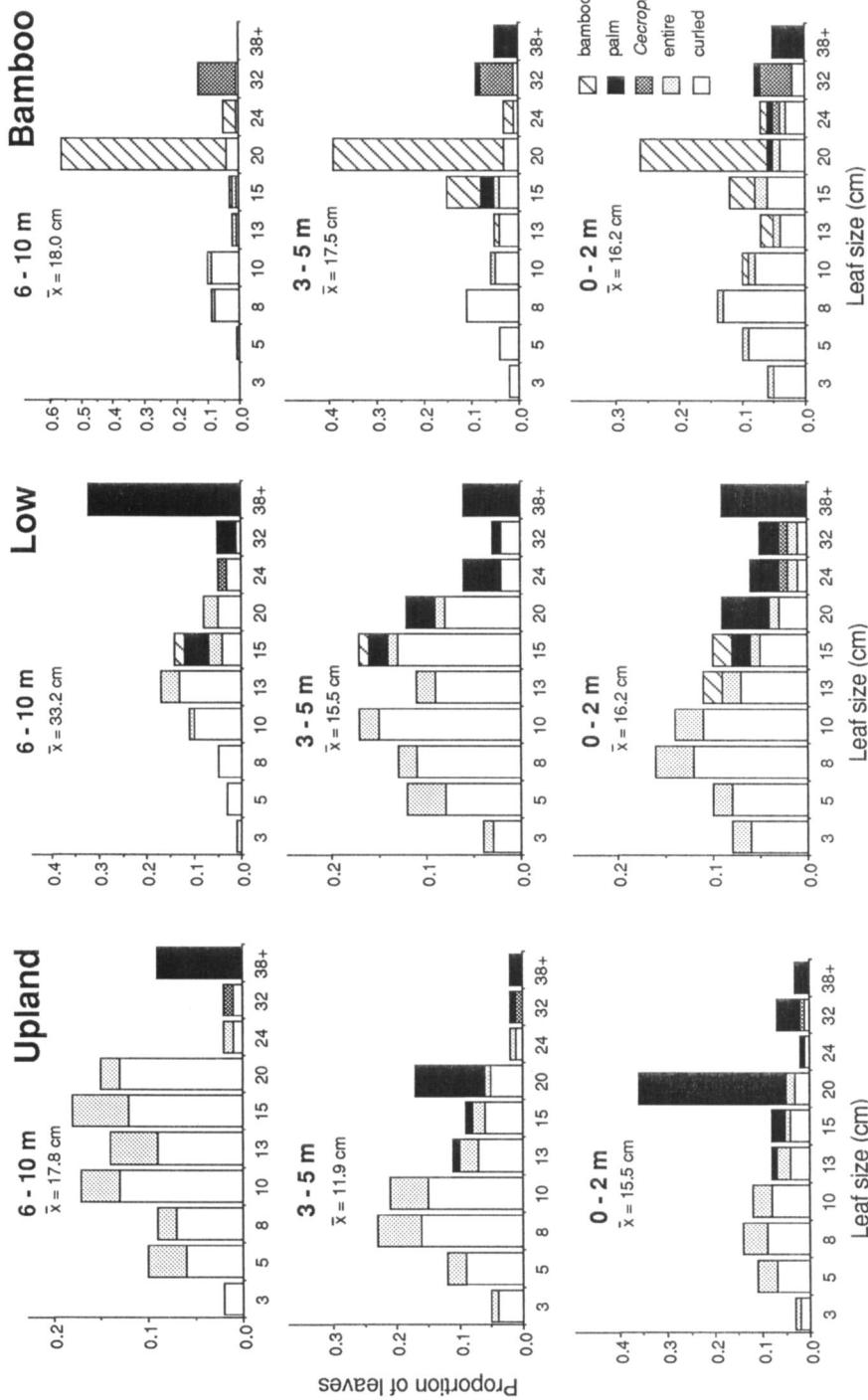


FIG. 4. Distribution of dead-leaf sizes and types at three height levels (0-2 m, 3-5 m, 6-10 m) in three Amazonian forest habitats. Based on 7417 leaves in Upland forest, 7794 leaves in Low-lying forest, and 9025 leaves in Bamboo. Average leaf size at each level is shown.

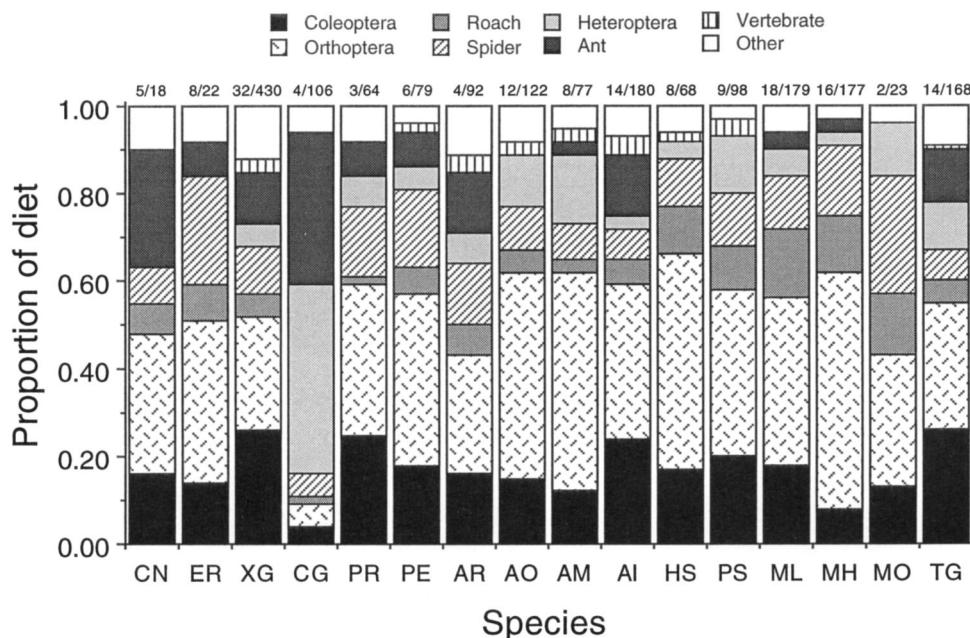


FIG. 5. Diets of 16 dead-leaf foraging birds in sw Amazonia. Bird species codes from Table 1. Sample sizes (above bars) are number of stomachs/number of prey items examined.

6), although much overlap existed for each prey category. Small antwrens generally did not take orthopterans larger than 20 mm, whereas the larger species ate many large as well as small orthopterans. *Xiphorhynchus guttatus* preyed on relatively small orthopterans for its size, however, overlapping greatly with the much smaller *Myrmotherula* spp.. All species preyed on relatively small spiders and beetles (Fig. 5b, c); in *Myrmotherula* spp. and *T. genibarbis*, virtually all beetles eaten were < 10 mm. The larger species ate beetles up to 18 mm long; in *X. guttatus*, which ate the highest proportion of beetles, nearly half were > 10 mm. *Craniolaeca gutturalis*, which ate mostly homopterans and ants, had the smallest overall prey size.

Prey-size diversity, based on the frequency distribution among 5-mm size classes, was lowest in *C. gutturalis* (1.97) and highest in *A. ochrolaemus* and *H. subularis* (5.60-5.63); all other species ranged from 3.28 to 4.98 (Table 3). Average prey-size diversity was similar in the two forest types (4.14 vs. 4.36).

**Prey availability.**—The arthropod fauna found in suspended dead leaves consisted mostly (>70%) of roaches, other orthopterans, spiders, and small beetles (Fig. 7). Also consistently present were ants (mostly colonial nesters), heteropterans, parasitic wasps, tiny flies, and a few moths and larvae. Four tree-frogs were also found inside curled dead leaves. Samples were similar among habitats, study sites, seasons, and years (Rosenberg 1990b).

Arthropods found in live foliage differed considerably from those in dead leaves (see Rosenberg 1990a, 1993). No roaches were found on live leaves, and fewer orthopterans and beetles. Spiders were about equally abundant on dead and live leaves, but ants, bugs, flies, and wasps were more numerous on live vegetation.

About one-half of the dead-leaf arthropods were  $\leq 5$  mm in length, including most beetles and nearly all flies, wasps, and ants (Fig. 7). Medium-sized (6–10 mm) prey consisted of orthopterans, roaches, spiders, and some beetles, whereas only orthopterans and roaches were among the larger available prey. Virtually all arthropods > 20 mm were katydids (Tettigoniidae).

The number of arthropods per dead leaf varied according to leaf type and size (Fig. 8). Abundance was highly correlated with leaf size in every habitat and seasonal sample. *Cecropia* leaves nearly always contained at least some arthropods ( $x = 1.34/\text{leaf}$ ), whereas entire leaves supported virtually none (0.04/leaf). Number of prey in palm leaflets was slightly above the overall average, whereas number in bamboo leaves was slightly below average.

I estimated overall arthropod density for each habitat at Tambopata by multiplying the density of prey in each leaf type by the abundance of that leaf type in each habitat, excluding entire

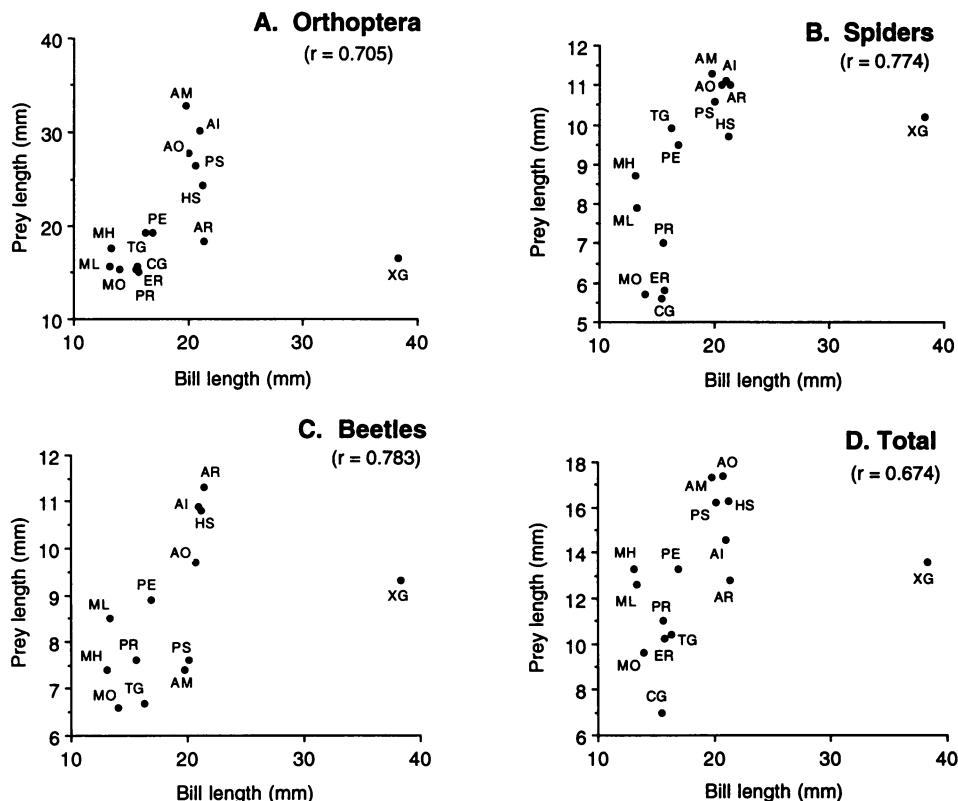


FIG. 6. Relationship between prey size and bill size among dead-leaf foraging birds. Data are the average lengths of prey eaten by each species. Bill length is the exposed culmen, averaged for five male and five female specimens. Correlations based on all species except *Xiphorhynchus guttatus*. Bird species codes from Table 1.

leaves. In May 1987, prey density was identical in upland and low-lying forest (0.29/leaf), but higher in bamboo (0.40/leaf). In July 1987, arthropod density in low forest had not changed (0.27/leaf), even though leaf abundance increased by 50%. In July 1988, however, prey density in this habitat increased to 0.37/leaf. Density of prey on live foliage at Tambopata (based on 3,155 leaves) averaged 0.10/leaf. Despite this 3–4 fold increase in number of arthropods from live to dead leaves, density per cubic meter of space was nearly identical for prey in live ( $6.3/m^3$ ) and dead ( $6.1/m^3$ ) foliage.

*Diets versus prey availability.*—The dietary composition of all bird species sampled differed significantly from prey availability in the dead leaves (Fig. 9). In nearly all species, orthopterans were highly selected, and except in the small antwrens, roaches were seemingly avoided. Other prey categories were usually eaten roughly in proportion (+ or - 10%) to their availability. The diets of *A. rufipileatus* and *X. guttatus* most closely matched the arthropods present in dead leaves, whereas that of *C. gutturalis* was highly divergent (not shown).

*Overall niche relationships.*—A summary of the ecological similarities within the dead-leaf foraging guild is illustrated by combined measures of overlap in resource space and diet (Fig. 10). Although roughly twice as many species were supported in low-lying forest, average overlaps in the two forest types were nearly identical. Considering overlap in resource space, the primary division in each habitat was between understory and canopy species, with greater overall separation among the latter species due to foraging on substrates other than dead leaves. A close ecological similarity among congeneric *Automolus* and *Myrmotherula* species was apparent in low-lying forest.

Combined overlaps in diet were generally much greater than overlaps in resource space. In each forest type, the most similar species consisted of most or all of the highly specialized antbirds and ovenbirds, as well as the more generalized *P. stellaris* and *X. guttatus*. Also, no

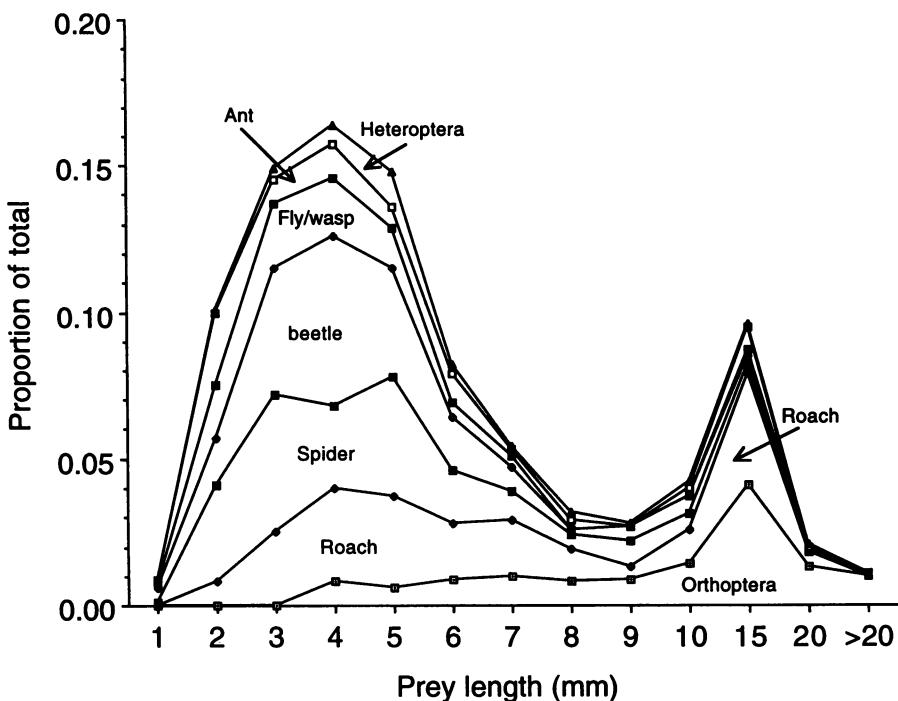


FIG. 7. Composition and size distribution of arthropod prey in suspended dead leaves in Amazonian forest. Based on 1025 arthropods collected from dead leaves at Pando, Bolivia and Tambopata, Peru.

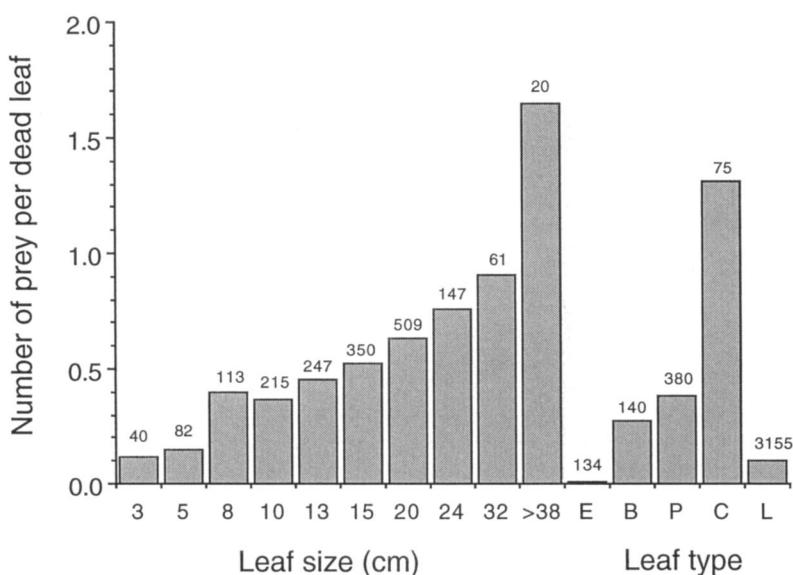


FIG. 8. Abundance of arthropod prey in dead leaves of different sizes and types. E = entire (uncurled); B = bamboo; P = palm; C = *Cecropia*; L = live leaves. Numbers above each bar indicates number of leaves sampled.

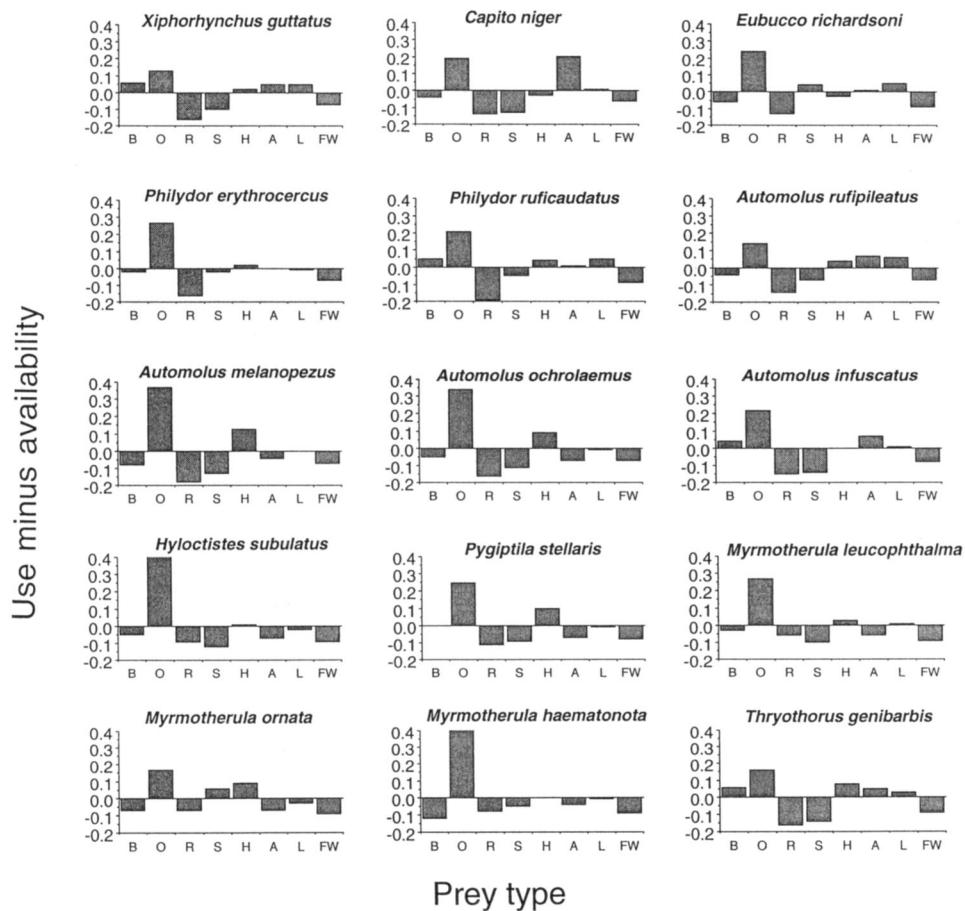


FIG. 9. Diets of 15 dead-leaf foraging birds compared with prey availability in suspended dead leaves. Horizontal line (0.0) indicates use = availability; bars above the horizontal indicate selection of prey, bars below indicate avoidance.

consistent segregation in diet was apparent between understory and canopy species. The most clearly divergent member of the guild was *Cranioleuca gutturalis*.

Similar conclusions can be reached by summarizing significant differences in foraging and diet measures (Appendix). The fewest differences overall were among *Automolus*, *Myrmotherula*, and *Philydor* species, whereas the most divergent species were *X. guttatus*, *T. genibarbis*, and especially *C. gutturalis*.

## DISCUSSION

**Contribution to avian species richness.**—The species that I studied, although extremely specialized in their foraging, are by no means rare or restricted geographically. In fact, dead-leaf searching species are a common and conspicuous component of Amazonian forest avifauna. At Tambopata, of roughly 150 insectivorous bird species, 17 species (11%) are dead-leaf foragers (11 are specialists by Remsen and Parker's criterion). These represent 18% of the 93 species that regularly join mixed-species foraging flocks. In 77 understory flocks that I censused at Tambopata (4–20 species per flock), an average of 36% of the species in each flock were dead-leaf foragers, with up to seven species in a single large flock. Thus, not only do these species contribute to the overall regional species diversity, but they also comprise a substantial proportion of the flocking insectivores at any point and time.

These results probably apply equally to the avifauna at Pando and at other Bolivian sites sampled by Remsen and Parker (1984). In 25 understory flocks censused by Munn (1985) at Manu National Park in southern Peru, an average of 23% of the species in each flock were dead-

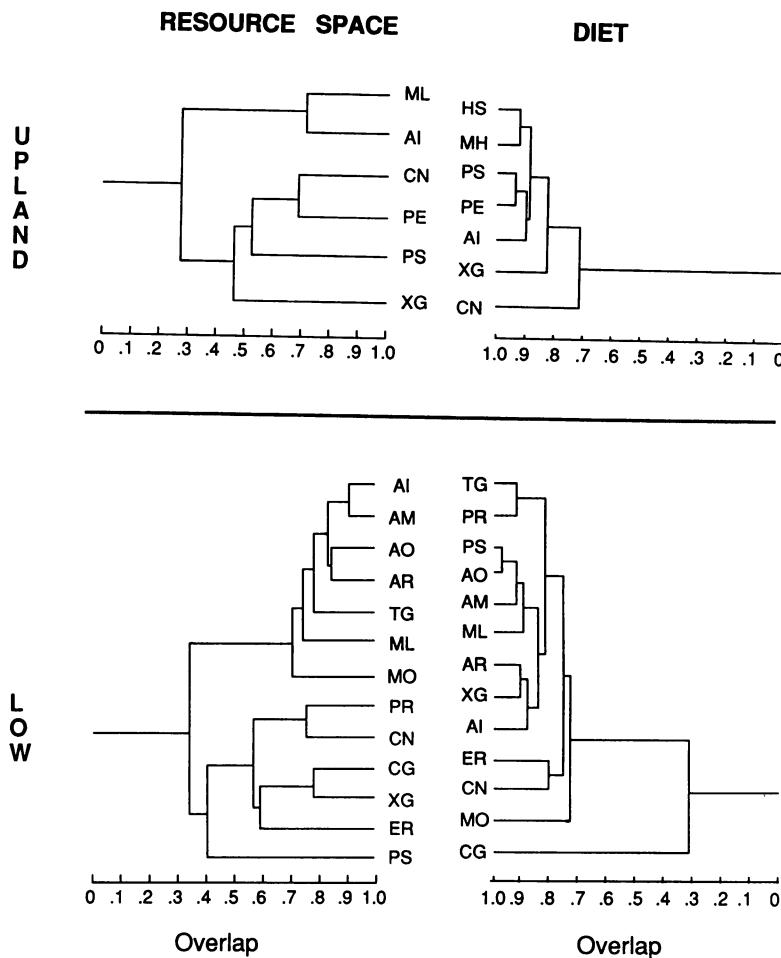


FIG. 10. Ecological overlap among dead-leaf foraging birds in two forest habitats in sw Amazonia. Overlap in resource space = O (foraging height) multiplied by O (substrate); Overlap in diet = O (diet composition) multiplied by O (prey size). All original overlaps based on proportional representation of 10 categories for each measure (see text). Phenograms constructed by computer program "PHYLIP" (Felsenstein 1987). Species codes from Table 1.

leaf foragers; this value is lower perhaps because the censuses were over longer periods and included many species that only occasionally joined a particular flock. Munn's data (1985) also indicated that up to seven dead-leaving species occurred in a single flock. Thiollay (1988), working in the opposite corner of the Amazon Basin in French Guiana, calculated that 23% of the prey attacks by 13 common, understory, foliage-gleaning species were at dead leaves. Four of the 13 species in that study were probably dead-leaf specialists.

In lowland forests of Central America, dead-leaving *M. fulviventer* helps to form the nucleus of typical mixed-species foraging flocks (Gradwohl and Greenberg 1980). Other dead-leaf specialist genera (e.g. *Eubucco*, *Automolus*) are represented by at least one species in Panama and Costa Rica, in some cases by the same species that is widespread throughout Amazonia. In southwestern Costa Rica, as many as five dead-leaving species may join a single understory flock (Rosenberg, pers. obs.). Therefore, in spite of geographic differences in total species number, the presence of a dead-leaf foraging guild that is a core component of mixed-species flocks appears to be constant throughout most Neotropical lowland forests. A decline in the importance of dead-leaf foraging is seen only with increasing latitude outside the tropics and with increasing elevation in the South American Andes (Remsen and Parker 1984). The extent to which this

phenomenon is restricted to Neotropical as opposed to Asian or African forest communities is unknown.

*Niche segregation among dead-leaf specialists.*—Two factors may influence the subdivision of this already specialized resource: the distribution and productivity of specific resource types and interactions with potentially competing guild members. As shown by Rosenberg (1990a), most understory birds selected dead-leaf types nonrandomly, avoiding very small leaves and selecting large and distinctive leaf types in each habitat. Avoidance of small leaves was explained by their low productivity in terms of prey availability. To some extent, most species showed evidence of exploiting the most abundant substrate types available. In spite of this general tendency for the guild to track resources in each habitat, virtually every species pair differed significantly with respect to substrate type, leaf size, or foraging height (Appendix). This pattern initially suggests that, in addition to responses to resource availability, species-specific foraging niches in this guild are influenced by co-occurring species.

The only consistent pattern of dietary differences among these birds was in prey size. Each major prey group was partitioned, at least by small versus large bird species. Large orthopterans were the most important prey for all species, and size of orthopterans eaten was highly correlated with bill size (except in *X. guttatus*). Thus, of all the niche parameters measured, only the difference in bill size was a useful predictor of dietary differences within this guild. This contrasts with a study of four woodcreepers from the same study sites (including *X. guttatus*), in which bill size was unrelated to prey size (Chapman and Rosenberg 1991). It is possible, however, that many small prey represent nymphal stages of the same katydid species eaten as adults by large birds, such that predation by the smaller species may potentially reduce prey availability for larger species at a later time.

Because the arthropod fauna of dead leaves was relatively uniform, even across habitats and sites, it is perhaps no surprise that all species searching dead leaves would have similar diets. Subtle differences in foraging height or behavior may be important, however, in reducing spatial overlap among birds in the same flock, thus affecting interference rather than exploitative competition. If so, then species with the most similar foraging niches might be expected to avoid feeding in the same flocks, thus contributing to a "checkerboard" distribution of species among flocks (Graves and Gotelli 1993). This was partially true, to the extent that several pairs of congeners segregated completely by habitat and did not occur syntopically. However, within each habitat, I found no negative spatial associations between any species pairs, suggesting that these birds joined flocks independent of the other species present and independent of their ecological similarity. This result is partly in conflict with Graves and Gotelli's (1993) analysis of Munn's (1985) flock data, which found a significant checkerboard distribution pattern in several ecological groups of congeners, including dead-leaf foragers.

Of particular relevance, then, is the degree of interaction among ecologically similar congeners. In low forest at Tambopata, *M. leucophthalma* shared the understory with *M. ornata*, and a potential further segregation in habitat did not take place. The two antwrens occurred together in 23 of 45 understory flocks in areas with at least some bamboo. In this habitat, *leucophthalma* and *ornata* differed significantly in average foraging height, leaf size, and substrate use (Appendix). The most striking difference was the avoidance of bamboo leaves by *leucophthalma*, even though this species frequently used bamboo leaves where it occurred alone at Pando. Further south in Bolivia, in the absence of *leucophthalma*, *ornata* becomes a habitat generalist in forest with little bamboo (Remsen and Parker 1984; J. V. Remsen and S. M. Lanyon, unpubl. data).

It is tempting to cite this as evidence for ecological release and competitive interactions among these antwren species. However, when foraging together, the two species, on average, converged in foraging height and overlapped more in substrate use than when apart (Rosenberg 1990b). This convergence may indicate a shared response to local resource conditions and is consistent with my observation that most members of any mixed-species flock forage at approximately the same heights at any particular time. Differences between the two species when together were still significant, however, suggesting that subtle, relative height differences are maintained. It is noteworthy that in 598 observations of these two antwrens together at Tambopata, I noted only a single mildly aggressive interspecific encounter, a female *ornata* briefly chasing a *leucophthalma*. On many occasions, however, the two species fed in close proximity (sometimes on the same branch) without interacting in any way.

A different situation existed among the *Automolus* foliage-gleaners. As noted above, because of habitat segregation these species rarely occurred together in the same flock. When two species did forage together, however, divergence in foraging height was striking (Rosenberg 1990b); in four flocks their foraging heights were completely nonoverlapping. Furthermore, in one flock, I

observed prolonged physical aggression between an individual *A. ochrolaemus* and *rufipileatus*, and in a second flock both birds vocalized frequently, giving calls normally used in intraspecific encounters. The more aggressive nature of *Automolus* species, compared with *Myrmotherula* species, is supported by additional observations of individuals fighting with *Pygmyptila stellaris*, and displacing smaller antwrens from specific foraging sites. At nearby Manu National Park, Robinson and Terborgh (1995) found *Automolus* species pairs to exhibit a range of interspecific territorial behavior, from nonoverlapping to complete overlap. Among overlapping species pairs, assymetrical aggression was noted, with the species occupying the later-successional stage of habitat (i.e., more mature forest) usually dominating.

Niche segregation within the dead-leaf foraging guild appears to represent a dynamic balance between the constraints imposed by feeding in a mixed-species flock and those imposed by feeding close to potential competitors. The former may lead to convergence in foraging height and substrate use, both as a shared response to resource conditions and as a means of deriving the maximum benefit from group vigilance. At the same time, divergence should be expected if competition for shared resources is important.

Each species (or set of species) may solve this apparent dilemma in different ways. In *Myrmotherula* antwrens, local syntopy at Tambopata is tolerated without overt aggression or divergence of niches within individual flocks. In contrast, the same level of niche segregation in *Automolus* foliage-gleaners is apparently rarely sufficient to allow syntopy. Near total segregation is maintained through habitat differences, niche divergence within flocks, or aggression. Possibly, the relative rarity of large leaves and large orthopterans within those leaves increases the potential for competition among the larger species. This also supports Powell's (1989) suggestion that smaller species may underutilize food resources and coexist with greater niche overlap in flocks because the flock's territory size is determined by the needs of the larger species.

*Maintenance of dead-leaf specialization.*—The ubiquity of dead-leaf foraging in lowland tropical forests is certainly related to the abundance and high productivity of aerial leaf litter. Although leaf distribution was extremely patchy, it is likely that the scale of that patchiness affected the movement patterns of individual birds within their flocks' territories more than the distribution of flocks. Overall availability of dead leaves did differ among forest types, however.

In upland forest at Tambopata, the lower average dead-leaf density and relative scarcity of high density sites, along with the smaller average leaf size and relative scarcity of novel leaves such as *Cecropia*, probably resulted in fewer dead-leaving species using this habitat and a lower density of understory flocks (based on encounter rate along trails). Whether individual flocks had larger home ranges in upland forest, or whether portions of the forest were not occupied by flocking birds, was not determined. Where understory flocks occurred, however, the proportion of dead-leaf specialist species was similar to that in the other habitats.

In contrast, bamboo thickets offered the highest density of leaf-types preferred by birds (nearly 50% more than in upland), the greatest number of *Cecropia* leaves, and the highest average density of prey per leaf. The addition of 3 or 4 species to the dead-leaving guild at Tambopata is probably a result of this added productivity of bamboo. The largest understory flocks at Tambopata, including all flocks containing pairs of congeners (see below), were in the vicinity of bamboo thickets. It is possible that resource availability for dead-leaving species that form the nucleus for many flocks determines, in part, the formation and distribution of these flocks in lowland forests.

Taxonomic composition of prey available in dead leaves, at least at the ordinal level, appears to vary little geographically, perhaps contributing to the uniformity of dead-leaving behavior from site to site. Gradwohl and Greenberg (1982a) found that 68% of the arthropods in dead leaves in Panama were roaches, other orthopterans, and spiders, and suggested that the species involved were unique to aerial leaf-litter. Similarly, samples from Belize contained 62% orthopterans (including roaches), 17% spiders, and 14% beetles (Greenberg 1987b). That prey abundance is far greater and average prey size higher in dead leaves than on live foliage is also supported by several studies (Gradwohl and Greenberg 1982b, Greenberg 1987b, Rosenberg 1990a). Greenberg (1987b) calculated a 153:1 difference in arthropod biomass in dead versus live leaves at several sites in the West Indies and Belize. In particular, the consistent availability of large orthopterans, especially katydids, seems important in supporting the dead-leaf foraging birds.

For dead-leaf specialists to remain resident in tropical forests, resource availability must remain relatively stable year-round. Boinski and Fowler (1989) found that the accumulation of aerial leaf-litter was the least seasonal aspect of forest phenology measured in a Costa Rican rainforest. Furthermore, arthropods in dead leaves were the only subset of the arthropod fauna

not to decrease during the mid-wet season, when other arthropods may be limiting to their predators (Boinski and Fowler 1989). Although my seasonal sampling was limited, arthropod availability in dead leaves at Tambopata seemed similar between late rainy season and mid-dry season, as well as between years and sites. Exclosure experiments in Panama indicated that the dead-leaf foraging birds themselves may deplete the arthropod resource by as much as 50% over a 6-wk period (Gradwohl and Greenberg 1982a). I found a high degree of turnover of arthropods at individual leaves, however, with a leaf recolonized, on average, 3–4 days after prey removal (Rosenberg 1990a). It is likely that birds may re-visit individual leaves every few days with reasonable probability of success.

Seasonal variation in dead-leaf abundance existed at many sites at Tambopata, but this variation was generally less than that among sites within a season. New leaves accumulated locally at the start of the dry season as deciduous canopy trees became bare and as high winds associated with austral winter storms redistributed leaf clusters and opened up areas with new treefalls. The short-term effect of this seasonal change was to superimpose a temporal aspect on the already highly patchy spatial distribution of dead leaves. The long-term effect, particularly of high winds, is to maintain a broken canopy and promote the growth of dense vine tangles and bamboo thickets (Erwin 1985), which in turn enhances the accumulation of aerial leaf litter. On a regional basis, it is perhaps no surprise that the highest diversity within several dead-leaf foraging genera (e.g., *Automolus*, *Myrmotherula*) lies in a belt across southern Amazonia and along the base of the Andes, where exposure to windstorms and presence of bamboo is most pronounced.

**Costs of dead-leaf specialization.**—Although the benefits of specializing on an abundant, predictable resource are relatively easy to quantify, the possible costs that may constrain such behavior are more difficult to evaluate. One likely constraint is the apparent dependency of most specialists on mixed-species foraging flocks. Several qualitative lines of evidence suggest that flocking by dead-leaf foragers is related to their reduced opportunities for vigilance while feeding. Searching dry, dead leaves frequently involves noisy rummaging that is audible to an observer (and presumably a predator) beyond the range of visual contact. In addition, the birds frequently insert their bills and heads inside leaves or dark clusters, sometimes for relatively long time periods, and scan more distant areas only when travelling between leaves. This contrasts with most other species, which constantly search more distant live-leaf surfaces and adjacent airspace (Rosenberg, pers. obs.). These latter species, because of their tendency to spot predators, sometimes serve as sentinels and are usually the first to give alarm calls that potentially warn other flock members (Munn 1986). This tendency is especially well-developed in certain species (e.g., *Thamnomanes* antshrikes; Schulenberg 1983) whose vocal repertoire includes specific alarm calls that elicit immediate and often dramatic anti-predator responses in other flock members, including dead-leaf foraging birds. The dead-leaf foragers are often vocally silent while foraging and do not frequently give alarm calls.

These observations, although largely anecdotal, suggest that dead-leaf specialists may benefit directly from increased vigilance provided by mixed-species foraging flocks. Foraging in mixed-species flocks, however, may impose costs on dead-leaf foragers in several ways. First, the rate at which flocks normally travel may be greater than that most efficient for exploiting dead leaves. Thiollay (1988) recorded lower foraging rates (moves/minute) in dead-leaving *M. gutturalis* (12.0) than in 3 live-leaving *Myrmotherula* species (18.3–18.9). Birds foraging rapidly must flit from leaf to leaf and only cursorily inspect each one. In 23 leaves previously inspected by 9 different *M. leucophthalma* at Tambopata, I found 4 potential prey items remaining, suggesting that the hidden prey sought by these birds may be difficult to detect. On several occasions I observed dead-leaf foragers that lagged behind a flock to extract large prey from tightly curled leaves or to manipulate and eat prey after capture, efforts that sometimes required several minutes. Typically in these cases, the birds would then fly directly to join the distant flock, which was often still audible. Pairs with dependent young may find it particularly difficult to forage efficiently with a flock. Most of my observations of antwrens feeding away from flocks were of family groups, and in several instances families moved temporarily with a flock but then lagged behind. Whether these constraints affect dead-leaf specialists more than other species is unknown.

Another potential cost of joining a mixed-species flock is the close proximity of possibly competing species, especially other dead-leaf foragers. The presence of more than one specialist in most flocks may necessitate the subdivision of an already restricted source (as documented in this study), and may require the retention of at least some plasticity in resource selection. Intraspecific competition may be reduced in flocks, however, because for most species member-

ship is restricted to one pair or family group per flock. The flock thus serves as a basis for spacing and territorial establishment (Powell 1989).

An obvious consequence of extreme resource specialization is the potential vulnerability to a decrease in resource abundance or availability. Although dead leaves are a seemingly ubiquitous resource, their accumulation as aerial litter is in part dependent on the structure of the forest. It is noteworthy that nearly all dead-leaf specialist birds are restricted to primary lowland rainforests, a trait shared with most other insectivorous, mixed-flocking species. Some species inhabit naturally disturbed sites within forests, such as bamboo thickets, but only nonflocking *T. genibarbis* (and other *Thryothorus* spp.) occur in severely disturbed, nonforest habitats. Thus, the mutual dependency by dead-leaf specialists and other flocking species on a variety of resource types in intact forests may signal a shared vulnerability to human-induced disturbances.

Finally, a potential cost of extracting large prey hidden in curled leaves is danger from the prey itself. Large katydids and spiders in particular often have sharp spines on their legs or body and can give a nasty bite (pers. obs.). In cage experiments with *Myrmotherula* antwrens (Rosenberg 1993), dead-leaf specialist species were more willing and able to attack large orthopterans (>30mm) than were live-foliage-gleaning species. The largest prey (up to two-thirds the length of the bird's body) were often killed and eaten with great difficulty over long time periods (up to 45 min). Ability to handle these large prey may be an additional specialization of small dead-leaf foragers.

*Evolution of dead-leaf specialization.*—Most of this paper has been devoted to the ecological factors affecting species-specific behaviors and niche segregation among species. Those factors important in maintaining specialization, however, may not be the same as the evolutionary forces shaping long-term, genetically based foraging niches (Futuyma and Moreno 1988, Sherry 1990). By comparing species under variable ecological conditions, such as in different habitats or geographic locations, I hoped to identify the most stereotyped and flexible aspects of their behavior. Highly stereotyped behaviors are probably evolutionarily fixed, whereas behavioral flexibility may still be available for modification by natural selection or genetic drift.

Most dead-leaf foragers appear to be highly stereotyped in a qualitative sense; that is, their overall degree of specialization (dead vs. live leaves), modes of searching dead leaves (e.g., hanging postures, manipulative use of the bill), general foraging strata (understory vs. canopy), and diet composition do not vary substantially among individuals or populations. However, quantitative differences may exist in exact foraging heights or types of leaves searched. The ability (or need) to fine-tune these behaviors in response to subtly variable resource conditions or competitive regimes may have prevented further specialization over evolutionary time. In addition, more or less continuous gene flow among populations may prevent local specialization from occurring (Fox and Morrow 1981).

Specialized and stereotyped behaviors are thought to evolve most easily when resources are highly predictable. Aerial leaf litter and its component arthropod fauna appear to represent an extreme case of resource predictability, and dead-leaf foraging birds may be extreme in their stereotypy, even among tropical organisms. This system offers a stark contrast to many temperate-zone studies in which unpredictability and opportunism may be common (e.g., Wiens and Rotenberry 1979, Rosenberg et al. 1982). The extent to which this contrast reflects a true latitudinal gradient in resource stability remains to be shown with further comparative studies.

Important to the evolution of foraging specialization in these birds are psychological adaptations involving search images, learning, or memory. Greenberg (1987a, 1990) showed that the tendency to investigate novel substrates (including dead leaves) was inversely related to degree of neophobia, which was innate and varied among species. Greenberg (1987a) suggested that dead-leaf searching may represent a neotenic retention of curiosity towards novel substrates, which is usually more prevalent in young rather than in adult birds. Learning and the development of search images may enable individual organisms to become resource specialists and may be an important step in the fixation of these behaviors in populations. For example, Werner and Sherry (1987) documented that a "generalist" species, the Cocos Finch (*Pinaroloxias inornata*), was actually composed of specialized individuals (including dead-leaf specialists).

Ultimately, degrees of ecological specialization must be traced through phylogenetic lineages of species. Dead-leaf foraging obviously evolved independently in several families of birds; however, within each family only one or a few genera exhibit this behavior, suggesting strong phylogenetic constraints. Hackett and Rosenberg (1990) studied the genetic relationships among *Myrmotherula* and other small antwrens, including the dead-leaf specialists considered in this study. Genetic data clearly indicate that the "checker-throated" group of *Myrmotherula* (all dead-leaf specialists) represent a distinct clade (six species distributed throughout the Amazon basin,

Andean foothills, and southern Central America) not closely related to other *Myrmotherula*. In fact, the only other antbirds (of 12 genera tested) in the same clade as the dead-leaving *Myrmotherula* were *Pygiptila stellaris* and *Microrhopias quixensis*. The former species is a habitual dead-leaf forager, as documented in this study, and the latter is one of few other antbirds thought to be a regular user of dead leaves. Thus, we must conclude that this particular behavioral specialization represents a primitive trait that arose early in the history of this lineage, possibly more than nine million years before present (Hackett and Rosenberg 1990).

That dead-leaf specialization evolved before the radiation of the current species in independent lineages, and has remained qualitatively unchanged through these radiations, implies that the present-day ecology of these species may be irrelevant to the question of what originally led to the evolution of this specialization. In groups in which not all species are specialized (e.g., *Philydor*), the evolution of dead-leaf foraging may be more recent, or even ongoing. In such cases, current ecologies may represent the range of conditions that led to specialization in other lineages, and phylogenetic analyses may enable us to track these avenues of change. Also, comparative studies of geographic variation (if any) in less specialized species, such as *Pygiptila stellaris* and especially *Xiphorhynchus guttatus*, may illuminate conditions under which specialization was most likely to have evolved.

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## APPENDIX

SUMMARY OF NICHE DIFFERENCES AND SPATIAL OVERLAPS AMONG DEAD-LEAFING SPECIES IN TWO AMAZONIAN FOREST HABITATS. ABOVE DIAGONAL ARE MEASURES THAT DIFFERED SIGNIFICANTLY BETWEEN SPECIES PAIRS (K-S OR G-TESTS;  $P < 0.01$ ; SEE ROSENBERG 1990B); H = FORAGING HEIGHT; S = SUBSTRATE; L = LEAF SIZE; D = DIET COMPOSITION; P = PREY SIZE. BELOW DIAGONAL ARE MEASURES OF SPATIAL ASSOCIATION (CRAMER'S V); \* =  $P < 0.05$ . SPECIES CODES FROM TABLE 1. NOTE THAT DIETARY COMPARISONS ARE NOT POSSIBLE FOR CG, PR, OR AR; PARTLY FRUGIVOROUS DIET OF CN AND ER ARE ASSUMED TO DIFFER FROM OTHER SPECIES

		A. Upland forest						B. Low-lying forest																		
		CN	XG	PE	HSLD	HSD	HSLP	HSP	SD	HSLD	HSLD	HSL	ML	PS	AI	AO	AM	AI	AO	AM	AI	PS	ML	MO	TG	
CN																										
XG		.000																								
PE		.000	.218																							
AI		.000	.000	.218																						
PS		.000	.667	-.005																						
ML		.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000		
		CN	ER	XG	CG	PR	AR																			
CN																										
ER		.308	HS	HSL	HSD	S	HSL	HSL	HSL	HSL	HSLD	HSLD	HS	HSD	HSL											
XG		-.099	-.005		SL	SD	HSLP	HS	HSL	HSL	HSLD	HSLD	HSLD	SL	SLD	HSL										
CG		.011	.054	-.055			HSDP	HSDP	HSDP	HSDP	HSLDP															
PR		.088	.532*	-.179	.163		HL	HL	HL	HL	HLD	HLD	HLD	H	H	HS										
AR		-.089	-.046	-.121	.036	-.115		HS	HS	HS	HD	HD	HD	SL	SL	HSLD										
AM		-.100	.025	.052	.091	-.009	-.138		HS	HS	SD	SD	SD	HS	HS	HSLD										
AO		.045	-.009	.105	.017	-.224	.264	-.038		HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS		
AI		-.121	-.119	-.185	-.061	.054	-.166	-.186	-.187		HS															
PS		-.005	.100	.250	-.032	.000	.039	.107	.000		HS															
ML		-.089	-.300	.033	-.102	-.149	-.091	.195	-.102		HS															
MO		-.225	-.115	.199	-.291	-.125	.240	.157	-.102		HS															
TG		-.072	-.122	-.129	-.133	-.093	.367	.027	-.129		HS															