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DIET SELECTION IN AMAZONIAN ANTWRENS: CONSEQUENCES OF SUBSTRATE SPECIALIZATION

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ABSTRACT.—I used an observational and experimental approach to investigate the dietary consequences of substrate specialization in six species of Amazonian antwrens (*Myrmotherula*). Three species (*leucophthalma, haematonota,* and *ornata*) foraged exclusively at curled dead leaves suspended above ground, *axillaris* and *longipennis* foraged on live foliage, and *hauxwelli* was a substrate generalist, feeding at both live and dead foliage. Diet composition of all species was qualitatively similar, with soft-bodied orthopterans consistently the most important prey type. Dead-leaf specialists took other prey roughly in proportion to their availability in dead leaves, whereas diets of live-leaf foragers differed greatly from prey available on live foliage. Dead-leaf specialists also ate larger prey and especially larger orthopterans than did other antwrens. Substrate generalization in *hauxwelli* was associated with higher diet breadth and greater heterogeneity among individuals, compared with substrate-restricted foragers. Diet breadth was negatively correlated with prey size across all six species. When tested in outdoor cages, live-leaf foraging and generalist species showed little interest in dead- or live-leaf substrates, whereas all dead-leafers repeatedly inspected and manipulated dead and curled leaves in the absence of food. All foraging groups showed a similar degree of selectivity of prey types in feeding trials. Dead-leaf specialists did not differ from other species in their preference for orthopterans of different colors, although specialists were better able to catch and handle the largest katydids (>30 mm). Individual *hauxwelli* (the generalist) showed elevated levels of exploration at dead leaves with food reinforcement, suggesting short-term plasticity in search behavior. I conclude that substrate specialization in these birds involves fundamental differences in search behavior, but is not accompanied by equivalent changes in prey selectivity or preference. Dead-leaf specialists search for suitable substrates and then inspect them for hidden prey, taking prey roughly in proportion to their availability. In contrast live-leaf foragers search directly for prey and select suitable items from the wider array of arthropods available on live foliage. Substrate-restricted foraging may reduce diet breadth and promote diet stereotypy in both groups, whereas the single most important factor promoting specialization on dead leaves may be the predictable abundance of relatively large orthopterans. *Received 25 November 1991, accepted 27 May 1992.*

DIET SELECTION in birds may be influenced by morphology, foraging behavior, microhabitat selection, innate food preferences, and availability of food resources. Studies relating avian diets to specific behaviors or microhabitats, however, have been few. For an assemblage of insectivorous birds in a northern deciduous forest, Robinson and Holmes (1982) concluded that diets were constrained by species-specific search tactics, as well as the distribution of prey among foraging substrates. In one of the only studies that considered diets of tropical insectivorous birds, Sherry (1984) also concluded that specific predator-prey interactions were important in shaping foraging niches. In this study, I investigated the effect of foraging specialization on diet selection in an assemblage of morphologically and ecologically similar antwrens (*Myrmotherula* spp.) that inhabit the understory of primary Amazonian rain forest.

Foraging specialization is thought to promote coexistence in complex communities, especially among tropical forest birds (Orians 1969, Terborgh 1980, Remsen 1985). The extent to which such specialization results in dietary differences among species is not well known. If specialized behaviors restrict a bird's access to prey or limit its exposure to certain prey types, coadaptations between such predators and their prey may potentially evolve, possibly leading to innate prey preferences. If, alternatively, specialized be-

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haviors serve to partition foraging space without subsequent segregation of diet, the role of resource-based interactions in promoting specialization is less clear.

The antwrens I studied have been the subject of several ecological investigations (Wiley 1971, 1980, Pearson 1977, Jones 1978) that have reported subtle differences in behavior and foraging heights thought to allow coexistence among species. These species range in size from 7 to 10 g, and are virtually identical in bill length (15-16 mm). Most antwrens are typical gleaners of live foliage; however, several species are highly specialized searchers of curled dead leaves suspended above the ground (Remsen and Parker 1984, Gradwohl and Greenberg 1984, Rosenberg 1990a, b). Previous investigators (Gradwohl and Greenberg 1982, 1984, Rosenberg 1990a, b) concluded that dead-leaf specialist antwrens: (1) searched dead leaves in 98 to 99% of their foraging attempts; (2) selected foraging substrates (leaf types) and prey nonrandomly compared with that available; and (3) were exposed to different prey resources from antwrens that search live foliage. Therefore, substrate specialization may be important in promoting resource partitioning in these species, through dietary differences. Potential for interactions between specialist and nonspecialist species is enhanced because both typically join the same mixed-species foraging flocks and may feed side-by-side in a group-defended territory (Munn and Terborgh 1979, Munn 1985).

My study combined observational and experimental approaches to investigate the consequences of dead-leaf substrate specialization for diet selection. I first compared the behavior and diets of wild antwrens, asking: (1) do dead-leaf specialist species differ in diet composition and prey size from live-leaf foraging and generalist species; and (2) are prey types selected according to their availability in nature? Then, using a series of outdoor cage experiments on wild-caught antwrens, I asked: (1) do these species differ in their natural tendency to search or manipulate particular foraging substrates (dead versus live foliage); (2) are these tendencies influenced by food availability; and (3) do preferences for prey types under controlled conditions match these species' natural diets?

STUDY AREAS AND METHODS

Behavioral observations and experimental studies of antwrens were conducted over 10 months in 1987, 1988, and 1989 at the Tambopata Reserve, Department of Madre de Dios, southeastern Peru (12°50'S, 69°17'W; 290 m). This is an area of tall, primary Amazonian rain forest described further by Erwin (1985) and Rosenberg (1990b). I made additional observations during June through August 1986 in similar rain forest near Cobija, Department of Pando, northwestern Bolivia, about 200 km north-northeast of Tambopata. Also at the Pando site, birds were collected for dietary analysis as part of a general avifaunal survey by the Louisiana State University Museum of Natural Science (LSUMNS; Parker and Remsen 1987). Supplemental diet data came from birds collected at a few other sites in southwestern Amazonia, especially near Abujao, Department of Ucayali, Peru (LSUMNS stomach-contents collection).

I observed foraging antwrens by following individuals in mixed-species flocks, encountered opportunistically along forest trails. To minimize consecutive observations of individuals, I rotated my attention among several species in the same flock. For each bird I recorded species, sex, foraging height (estimated to nearest 1 m), method (glean, hover, etc.), substrate (including specific leaf surface and size), and perch type. My terminology for describing foraging behavior closely follows that of Remsen and Robinson (1990).

Diets were assessed from stomach contents preserved in 70% ethanol as soon as possible after collection. Samples were sorted and identified to lowest taxonomic level possible under a 6×-25× dissecting microscope. Minimum number of prey items in each category was determined from diagnostic fragments, such as mandibles (Orthoptera, larvae), fangs (spiders), heads, or wings (beetles, Heteroptera). I determined the proportions of prey categories in each individual stomach and then averaged these across individuals to determine the diet composition of each species (i.e. samples were not pooled). I compared diets among species using G-tests (Sokal and Rohlf 1981:704) based on the frequency distributions of prey categories, adjusted to reflect the average proportions of each prey category for each species. For example, the adjusted frequency of spiders for a species equaled the average proportion of spiders for that species multiplied by the total number of prey items in the sample. In some cases, stomach-contents data may not be appropriate for such statistical analyses because of potential nonindependence (i.e. pseudoreplication) among prey items in individual stomachs (Hurlbert 1984). However, because antwrens forage methodically and may search a variety of substrates between successful prey captures, and because identical prey types rarely appear more than once in any stomach, I believe it is appropriate to treat prey items as independent.

Prey size was estimated from the size of characteristic fragments using regression equations in Calver and Wooller (1982) and Diaz and Diaz (1990), or determined from voucher specimens from this study.

Prey-size distributions were compared among species using Kolmogorov-Smirnov (K-S) tests (Sokal and Rohlf 1981:714).

Diet heterogeneity was assessed in two ways. Overall dietary breadth for each species was computed as

$$B = 1/\Sigma\, p_i^2, \tag{1}$$

where p_i is the proportion of category i in the sample (Levins 1968). I used the average proportions of nine prey categories to calculate this measure. Also, as a measure of stereotypy among individual stomachs in each sample, I calculated population dietary heterogeneity (PDH) as the G-statistic (from matrix of nine prey categories for n stomachs) divided by degrees of freedom for that sample (Sherry 1984). This latter measure is thought to reflect evolutionarily constrained aspects of diet specialization rather than ecological response to resource availability (Sherry 1990).

Prey availability was estimated at Tambopata by searching individual dead and live leaves for arthropods, as described in Rosenberg (1990a, b). Samples of 1,918 dead leaves and 3,155 live leaves, all from within 3 m above ground, were used in this analysis. I compared frequencies of prey types in bird diets with availability samples using G-tests based on nine prey categories equally detectable in leaf and stomach samples. A significant difference in the distribution of prey types used and available was considered evidence of selectivity by that species.

Antwrens were captured for feeding experiments using mist nets placed in areas where flocks foraged. My initial attempts to keep birds in captivity for periods greater than one day were unsuccessful; therefore, prolonged periods of adjustment to captivity or repeated testing of individual birds was not possible. For this reason, only birds captured before 1000 EST were used as subjects, and only one individual could be used per day. Captured birds were immediately placed in the cage and allowed to adjust for about 1 h. The cage consisted of a frame of white plastic PVC tubing (0.5 × 0.5 × 0.5 m) covered with fitted mosquito netting and equipped with a closable opening on one side. Two diagonally oriented dead branches served as perches, and the cage was placed in the shade on the forest floor. Through trial and error, I determined that this small-sized enclosure worked best; birds were less distracted and more quickly became calm and accepted food.

After the initial waiting period, I placed several food items (usually small katydids) on the floor of the cage and again left the bird undisturbed for about 30 min (times varied among subjects). If after this period these prey were readily consumed, I began a series of feeding trials. For each trial I placed a previously identified and measured arthropod on the cage floor and returned to a spot roughly 10 m from the cage and partially concealed by foliage. I then closely observed the bird's response using 10× binoculars, timed each behavior with a stopwatch, and recorded these continuously onto a microcassette. Each trial lasted a maximum of 10 min, although I sometimes left uneaten prey in the cage during subsequent trials to see if initially rejected arthropods were eventually eaten. I scored each response on a subjective but unambiguous scale (Table 1), ranging from completely ignored (0) to eagerly and quickly consumed (4). To assure a wide array of possible prey offerings, my assistant and I captured arthropods using sweep nets, by searching live and dead leaves, and by searching along trails at night with lights. Some frequently used prey (e.g. katydids) were kept for several days in nearby enclosures. Still, the range of prey offered to each bird was limited by the day's "catch," and it was often not possible to replicate some prey types across all individuals.

Usually, after several successful feedings, the bird showed signs of searching for food in the cage between trials. At this point I began a series of substrate trials by attaching a dead leaf and a live leaf (or sprig of leaves) to the perches with wooden clothespins, without associated food. The positions of dead and live substrates were switched in successive trials. Again, I observed, timed, and recorded each response, and scored these on an unambiguous scale of behaviors (Table 1), ranging from ignored (0) to repeated physical manipulation of the leaves (5). I then alternated bouts of substrate and feeding trials until late afternoon, when the bird was released (usually about 1600). If time permitted, I combined substrates and prey in the same trial (i.e. prey were placed on or inside leaves) to observe changes in behavior or capture efficiency by birds feeding on "normal" versus "abnormal" substrates; for example, could a live-foliage species capture prey hidden in dead leaves, or could a dead-leaf specialist find cryptic prey on live leaves?

RESULTS

FIELD OBSERVATIONS

Foraging behavior.—Among the antwren species (*Myrmotherula*) I studied: *leucophthalma* (White-eyed Antwren), *haematonota* (Stipple-throated Antwren) and *ornata* (Ornate Antwren) used dead leaves almost exclusively; *axillaris* (White-flanked Antwren) and *longipennis* (Long-winged Antwren) used live foliage of various types; and *hauxwelli* (Plain-throated Antwren) was a substrate generalist, searching dead and live leaves as well as stems, ferns, and moss (Fig. 1). *Myrmotherula haematonota* occurred only at the Pando site, in upland forest, where it joined mixed-species foraging flocks with *axillaris* and *longipennis*. All species except *haematonota* occurred at Tambopata, and all species except *hauxwelli* regularly joined mixed-species flocks.

TABLE 1. Response scoring system used for captive antwrens offered a variety of substrates and prey types.

Score	Definition
	Substrates
0	Ignored.
1	Briefly looked at from short distance.
2	Closely inspected (but did not touch).
3	Touched surface with bill.
4	Manipulated or probed inside.
5	Repeated manipulation, probing, or tearing.
	Prey types
0	Ignored.
1	Initially attacked but rejected (did not eat).
2	Initially rejected but eventually eaten.
3	Tentative, hesitant, but readily eaten.
4	Very quickly attacked and eaten.

In both the dead-leaf and live-leaf foragers, the two co-occurring species differed slightly, but significantly, in average foraging height (Fig. 2; $t = 9.6$ for dead-leaf foragers, 4.0 for live-leaf foragers, $P < 0.001$); *haematonota* foraged lower at Pando than did the other dead-leaf-foraging species at Tambopata ($\bar{x} = 1.8$ m; not shown). *Myrmotherula longipennis* also used aerial maneuvers (e.g. hovering, sallying) more often than *axillaris* (73 vs. 58%). *Myrmotherula hauxwelli* foraged much lower than the other species (Fig. 2) and, typically, perched on thin, vertical stems (84% of observations). I never observed this species on the ground, however, in contrast with some other published accounts (e.g. Pearson 1977).

Diet composition and prey availability.—The diets of all six species were dominated (63–92%) by beetles, orthopterans (including roaches), and spiders (Fig. 3). Subtle differences in the proportions of prey categories, however, resulted in significant heterogeneity among species ($G = 166.2$, df $= 40$, $P < 0.001$). Pairwise comparisons, controlling α-level for multiple tests (Sokal and Rohlf 1981:721), revealed that the diet compositions of *ornata, axillaris, longipennis,* and *hauxwelli* did not differ significantly ($P > 0.02$). The diet of *ornata* also did not differ from *leucophthalma.* However, *haematonota* and *leucophthalma* did differ in diet from the generalist and live-leaf-foraging species ($P < 0.001$). In general, the dead-leaf-specialist species ate a higher proportion of orthopterans and roaches, whereas the two live-leaf foragers ate more larvae. The generalist *hauxwelli* showed the most varied diet, with the highest proportions of ants, flies, and wasps, as well as the fewest orthopterans.

Prey availability in dead leaves consisted

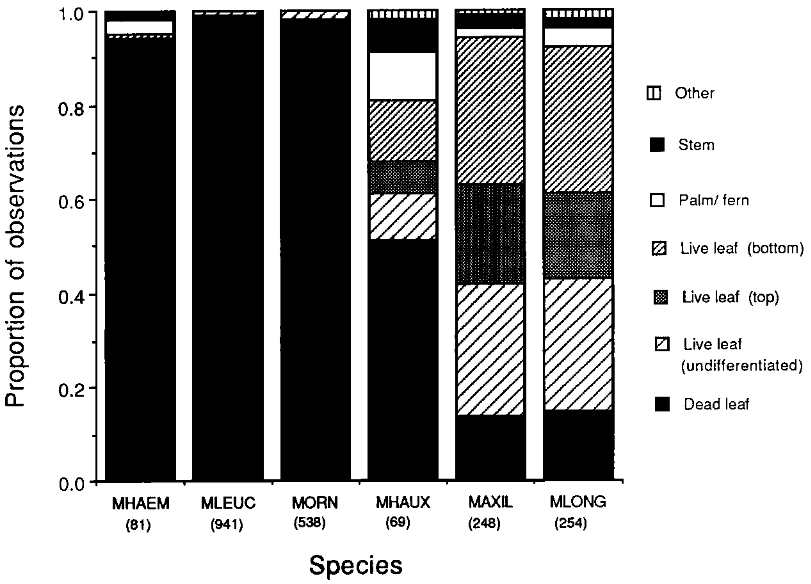

Fig. 1. Foraging substrate use by five species of antwrens of the genus *Myrmotherula*: (MLEUC) *leucophthalma*; (MORN) *ornata*; (MHAUX) *hauxwelli*; (MAXIL) *axillaris*; (MLONG) *longipennis*. Number of observations in parentheses.

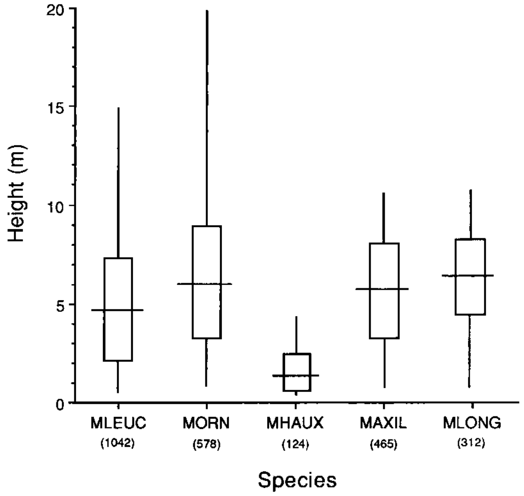

Fig. 2. Average foraging heights of five species of antwrens. Vertical bars indicate ±1 SD; vertical lines indicate range. Number of observations in parentheses. Species codes from Figure 1.

mostly (75%) of spiders, roaches, beetles, and orthopterans, whereas these made up only 35% of the arthropods on live foliage (Fig. 3). In contrast, one-half of the prey on live leaves were ants, flies, and wasps. In addition, 83% of arthropods in dead leaves were brown and 4% were green, compared with 38% brown and 18% green on live foliage. All orthopterans in dead leaves were brown, whereas 21% of those on live leaves were brown and 67% were green. Average size of all arthropods in dead leaves was significantly larger than those on live foliage (6.5 vs. 5.3 mm), as was the size of available orthopterans (12.9 vs. 8.0 mm). Over 50% of the orthopterans in dead leaves were greater than 10 mm, compared with 22% on live leaves. Thus, birds foraging on live and dead leaves are exposed to different proportions of prey types, as well as prey of different colors and size distributions.

Compared with prey availability, all species selected orthopterans (Fig. 4) and for all species, diet differed significantly from proportions represented in available prey (*G*-tests, $P < 0.001$). The dead-leaf specialists took other prey types roughly in proportion (±10%) to their availability in dead leaves. The two live-leaf foragers exhibited greater selectivity, eating more beetles and larvae than expected, and many fewer ants, flies, and wasps. The diet of *hauxwelli* differed from arthropod distributions on both dead and live leaves, but was closest to that on dead leaves.

The three dead-leaf specialists exhibited the narrowest dietary niche breadths (Table 2), whereas the generalist *hauxwelli* showed the

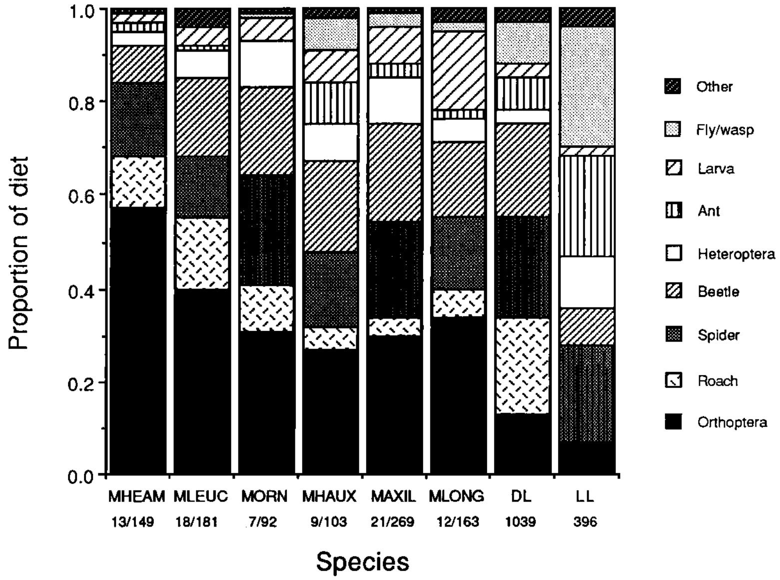

Fig. 3. Diet composition of five species of antwrens (species codes from Fig. 1) and composition of available prey on dead (DL) and live leaves (LL). Sample sizes for birds are number of stomachs/number of prey items, and for leaves are number of arthropods sampled.

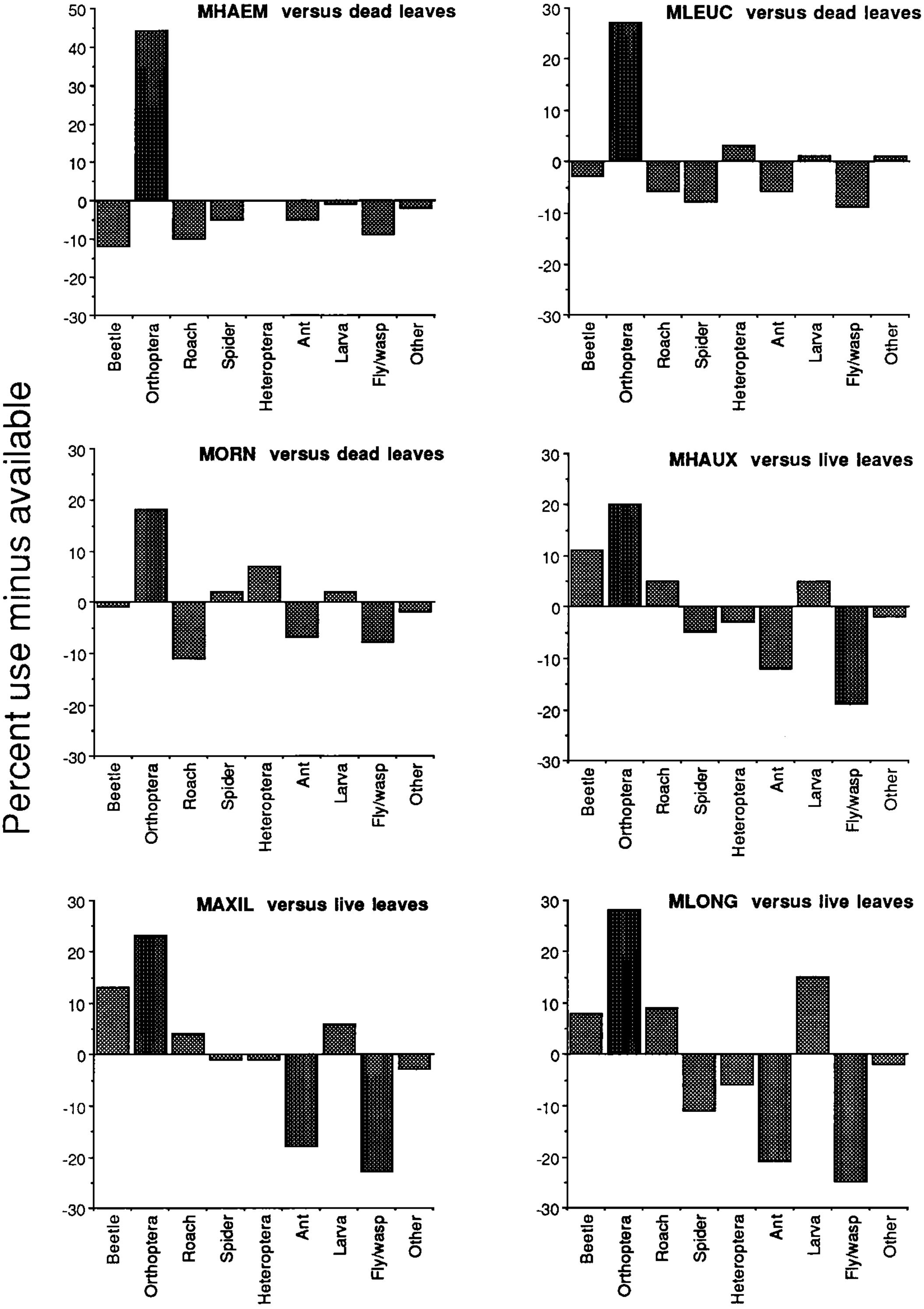

Fig. 4. Comparison of diet and prey availability for five species of antwrens. Horizontal line (at "0") indicates use equal to availability; bars above horizontal indicate selection and bars below horizontal indicate avoidance of prey. Species codes from Figure 1.

TABLE 2. Dietary characteristics of six Amazonian antwrens. Prey sizes are $\bar{x} \pm 1$ SD (number of prey items in parentheses).

Myromotherula	Diet breadth	Population dietary heterogeneity	Prey size (mm)	Orthoptera size (mm)
haematonota	2.70	0.77	13.3 ± 5.7 (139)	15.7 ± 5.1 (95)
leucophthalma	4.08	0.95	12.6 ± 6.6 (119)	17.6 ± 6.0 (56)
ornata	4.93	0.98	11.3 ± 6.0 (70)	16.1 ± 5.6 (28)
axillaris	5.15	1.00	8.8 ± 4.1 (169)	12.6 ± 3.5 (65)
longipennis	5.00	0.92	9.3 ± 5.0 (105)	13.5 ± 4.6 (47)
hauxwelli	6.18	2.15**	7.6 ± 6.6 (65)	12.6 ± 3.6 (17)

**, $P < 0.001$, (*G*-test).

highest diet diversity. In terms of heterogeneity among individuals (PDH), dead- and live-leaf foragers had similarly uniform diets. *Myrmotherula hauxwelli* showed greater heterogeneity, and only this value was associated with a significant *G*-statistic ($P < 0.001$). Population dietary heterogeneity for samples from a single site varied from 0.50 for *leucophthalma* from Abujao, Peru ($n = 5$) to 3.07 for *hauxwelli* from Tambopata, Peru ($n = 4$). In no species was PDH for the pooled sample greater than that for individual sites, suggesting that geographic variation did not contribute to overall dietary heterogeneity in these species.

Estimates of average prey size were larger in the dead-leaf-specialist than in the live-leaf foragers or the generalist (Table 2); differences were significant for all comparisons except *ornata* versus *longipennis* (K-S tests, $P < 0.05$). All three dead-leaf specialists also ate significantly larger orthopterans (as estimated from mandible size) than generalist or live-leaf-foraging antwrens (K-S tests, $P < 0.05$). The clearest distinction between these groups was in their predation on large orthopterans (>17 mm); these comprised 19 to 24% of all prey consumed by the dead-leaf specialists versus only 2 to 5% of prey in the other species. Across all six species, average prey size was highly, negatively correlated with diet breadth ($r = -0.912$, $P < 0.02$).

FEEDING EXPERIMENTS

I tested 17 individuals of five antwren species in the outdoor cage. These included seven dead-leaf specialists (five *leucophthalma* and two *ornata*), five live-leaf foragers (three *axillaris* and two *longipennis*), and five of the generalist *hauxwelli*. Because of the small sample sizes, all individuals of each foraging mode are combined in most of the following comparisons.

Substrate response.—The clearest distinction between species was in their response to dead- and live-leaf substrates, without associated food (Fig. 5). The two live-leaf-foraging species and the generalist showed little interest in either leaf type, scoring between 1.4 and 2.1 on my scale. Typically, individuals of these species inspected a leaf briefly from several centimeters away and then ignored it for the remainder of the trial. They rarely touched a leaf with the bill (10 of 43 trials), and in only 3 of 43 trials did an individual look inside a curled dead leaf for potential prey.

In sharp contrast, all individuals of the two dead-leaf-specialist species exhibited typical dead-leaf-searching behavior, repeatedly probing the bill or head inside curled leaves or picking at the leaves from several angles. Scores for individual dead-leaf specialists in response to dead leaves ranged from 3.9 to 4.8, and were significantly higher than scores for either of the other two foraging groups (K-S tests, $P < 0.001$). These results were significant if the two dead-leafing species were tested separately against

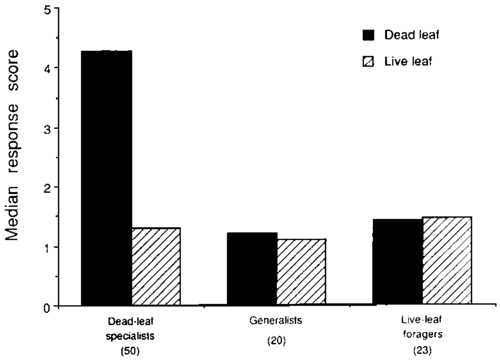

Fig. 5. Median response scores for three groups of captive antwrens presented with dead- and live-leaf substrates. Number of trials in parentheses.

TABLE 3. Prey selectivity by captive antwrens. Median response scores (with proportion of prey eaten in parentheses) for each of 12 prey categories.[a]

	Dead-leaf specialists ($n = 7$)		Generalists ($n = 5$)		Live-leaf foragers ($n = 5$)	
Prey type	N	Median (proportion)	N	Median (proportion)	N	Median (proportion)
Orthoptera						
Katydid/cricket	71	4.0 (0.93)	37	4.0 (0.92)	57	4.0 (0.84)
Grasshopper	39	2.0 (0.74)	38	3.0 (0.74)	18	1.5 (0.56)
Walking-stick	15	1.0 (0.40)	5	3.0 (0.80)	16	3.0 (0.75)
Roach	10	4.0 (1.00)	7	4.0 (0.86)	10	4.0 (0.90)
Spider	13	4.0 (0.92)	10	4.0 (0.90)	9	4.0 (1.00)
Beetle	17	1.0 (0.18)	9	0.0 (0.22)	7	0.0 (0.00)
Heteroptera	20	1.0 (0.26)	17	0.0 (0.24)	8	0.5 (0.38)
Ant	9	0.0 (0.00)	2	0.5 (0.00)	6	0.0 (0.00)
Butterfly/moth	10	3.5 (0.80)	2	2.5 (1.00)	7	1.0 (0.43)
Dragonfly	4	2.0 (0.50)	3	4.0 (1.00)	2	2.5 (0.50)
Fly/wasp	5	0.0 (0.00)	5	0.0 (0.00)	3	1.0 (0.33)
Larva	5	4.0 (1.00)	4	1.0 (0.25)	3	3.0 (0.67)
Average	217	2.2 (0.56)	140	2.2 (0.58)	146	2.0 (0.53)

[a] n refers to number of individuals tested, while N indicates number of prey items offered.

each of the other three species. Response scores for live leaves, however, were not elevated in the dead-leaf-specialist species. In six trials, I presented dead-leaf specialists with live leaves that were rolled or folded. Response scores were the same as for dead leaves (median = 4.2), with the birds picking at and probing inside the leaves for hidden prey.

Prey selectivity.—Individuals of each foraging group exhibited a similar degree of selectivity, based on 12 prey categories offered to each species (Table 3). All individuals readily ate roaches, spiders, crickets and small katydids. In most cases, these prey were immediately and eagerly captured and swallowed whole, sometimes before my hand was removed from the cage. Larger katydids also were usually captured immediately, but were taken to a low perch to eat (see below). Other orthopterans, especially hard-bodied or brightly colored grasshoppers (Acrididae), were either eaten after some initial hesitation or were rejected. Nearly all ants, flies, wasps, and most beetles and heteropterans also were ignored or rejected. Individuals of both dead-leaf-specialist and nonspecialist species ate butterflies and dragonflies, often pursuing them in the cage with uncharacteristic agility. Response to larvae was variable; samples of these prey were too small to draw any general conclusions.

In addition to these prey categories, I offered opiliones ("daddy long-legs") to *ornata* (1), *hauxwelli* (2), and *longipennis* (2); all were ignored. Finally, individual *hauxwelli* and *axillaris* each caught small lizards (total length ca. 50 mm), which were beaten on a branch and swallowed whole; neither *leucophthalma* nor *ornata* would eat small lizards or frogs, although a *leucophthalma* was very interested in a lizard that was apparently too large to catch.

Because orthopterans were an important food for all species, I further evaluated selectivity of these prey with regard to size, color, and background substrate. All species readily ate most orthopterans 25 mm or smaller in length (Fig. 6). Reaction to larger prey, however, varied among groups, with the live-leaf foragers eating fewer large prey. *Myrmotherula axillaris* ate only two of six katydids greater than 30 mm (maximum = 40 mm), and *longipennis* did not attack any of four katydids greater than 25 mm. In contrast, the two dead-leaf-specialist species collectively ate 11 of 12 katydids greater than 30 mm, including four that were 48 to 50 mm; these prey were more than two-thirds the length of the bird. In cases in which prey were not eaten, the birds usually showed great interest in the katydids, but either were hesitant to attack or seemed physically incapable of grabbing and subduing the prey. When these large prey were captured by one of the dead-leaf specialists, it was usually with great difficulty, sometimes taking up to 12 min for the bird to catch the katydid and up to 3 min to kill it (see data on handling times below). The birds would sometimes "give up" several times before even-

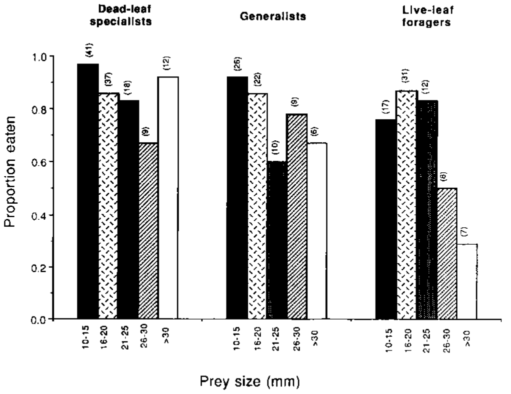

Fig. 6. Proportion of orthopteran prey of different sizes eaten by three groups of captive antwrens. Number of feeding trials in parentheses.

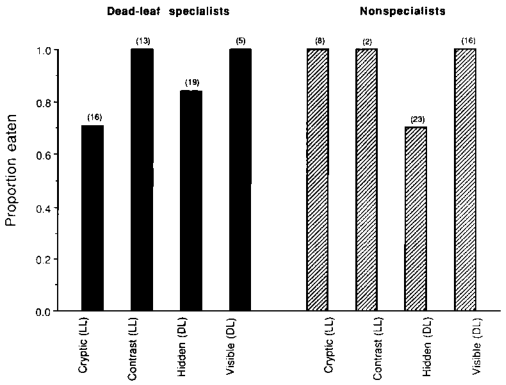

Fig. 8. Proportion of prey eaten by specialist and nonspecialist antwrens; prey were either cryptic (green) on live leaves (LL), contrasting on live leaves, hidden inside dead leaves (DL), or visible on dead leaves. Number of feeding trials in parentheses.

tually completing the kill, a situation unlikely to occur in the wild.

Response to prey of different colors was evaluated, considering only orthopterans less than 30 mm, to eliminate prey that were too large to eat. The proportion of brown versus green prey eaten did not differ among dead-leaf specialists, live-leaf foragers, and generalists (Fig. 7); in all cases, slightly more green than brown prey were taken. Both of these color groups were cryptic on their respective backgrounds of dead or live leaves. Prey of other (noncryptic) colors were eaten with lower frequency, at least in the live-leafing and generalist species.

Finally, I compared dead-leaf specialists with all other species as to their ability to locate prey on dead- versus live-leaf substrates. In these trials, prey were either cryptic (green) on live leaves, contrastingly colored on live leaves, visible on dead leaves, or hidden from view inside curled dead leaves. The dead-leaf-foraging species found 10 of 16 (71%) cryptic prey on live leaves and 16 of 19 (84%) prey hidden in dead leaves (Fig. 8). Nonspecialist species located all visible prey, but found only 16 of 23 (70%) that were hidden in dead leaves. The amount of time taken to locate prey was highly variable among trials and did not differ among species. My impression was that individual dead-leaf foragers often did not recognize cryptic prey hiding on live leaves and discovered them "accidentally" after jostling the leaves in the cage.

Behavioral flexibility.—In three individual *hauxwelli,* I tested for short-term changes in search behavior due to food reinforcement. In each case, after testing the bird's response to dead- and live-leaf substrates as described above,

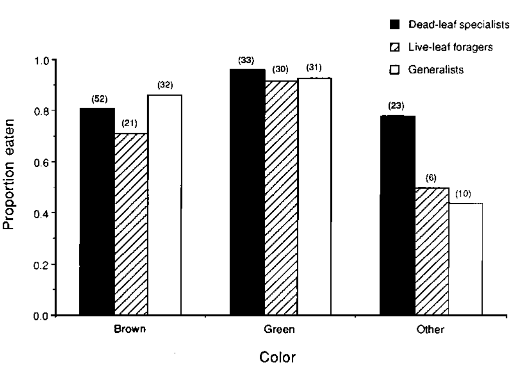

Fig. 7. Proportion of orthopteran prey of different colors eaten by three groups of captive antwrens.

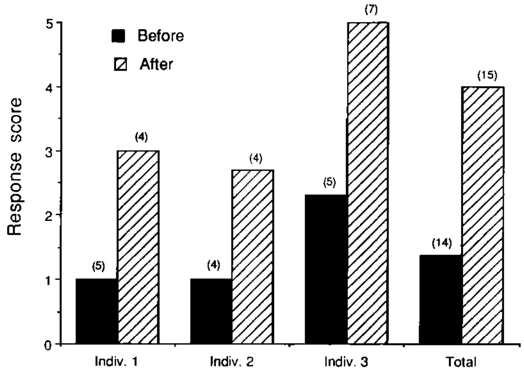

Fig. 9. Average response scores of three *M. hauxwelli* to dead-leaf substrates before and after receiving food in dead leaves; number of trials in parentheses.

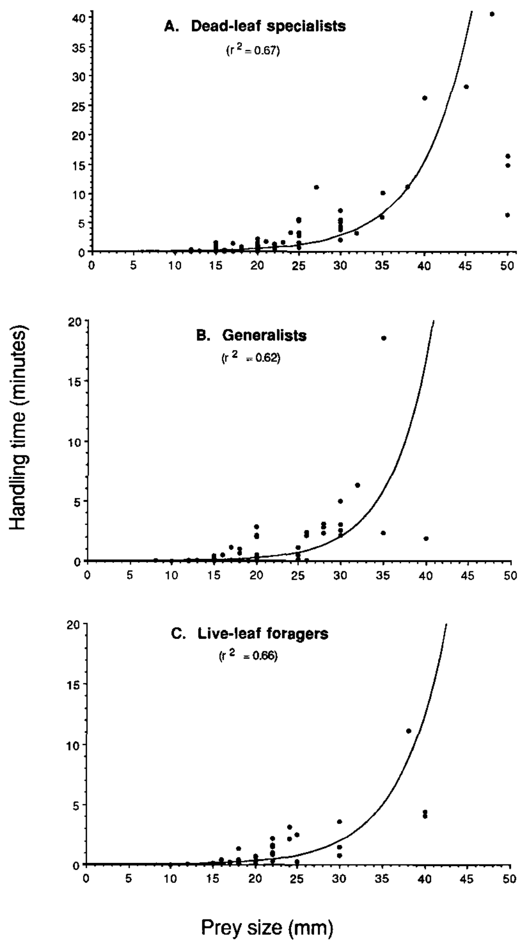

Fig. 10. Handling times for orthopteran prey in three groups of antwrens. Exponential curves fit by program Cricket-Graph (Macintosh).

I provided food only in the dead leaf. After 10 consecutive feedings, I retested these individuals' response to substrates in the absence of a food reward. In all three individuals, the response to dead leaves was higher after food was provided than before (Fig. 9). Individual 3 showed characteristic dead-leaf searching behavior after feeding at the dead leaf, repeatedly manipulating and probing inside leaves in all seven subsequent trials. The other individuals each manipulated at least one dead leaf after feeding, whereas neither had even touched a leaf with the bill before. Response to live leaves was not elevated in any bird. Although this small sample was not appropriate for statistical testing, it suggests that dead-leaf searching behavior may be induced by food reinforcement, at least in the generalist species.

Prey handling behavior and times.—All species exhibited similar modes of killing and eating arthropod prey. The most common method, used for all small prey, was to crush in the bill by working the arthropod sideways across the mandibles, and then to swallow it whole. Larger prey, especially large orthopterans, typically were taken to a low perch within 5 cm of the cage floor. There the bird would begin at the head and—by beating, shaking, and biting,—would eat the arthropod in pieces. Prey items were frequently dropped to the floor and retrieved from the low perch. After eating (or discarding) the head, the bird would eviscerate and eat the thorax from the head-end first, then break off and swallow legs, then eviscerate the abdomen, and finally after much beating and mandibulating, swallow the exoskeleton of the abdomen. This highly stereotyped process was also observed in wild antwrens eating large orthopterans.

Handling time for orthopterans up to about 20 mm was usually negligible, often under 10 s (Fig. 10). For larger prey, handling time increased sharply; usually, several minutes were required to dismember katydids larger than 25 mm, and up to 40 min were spent on the largest prey. A few orthopterans up to 26 mm were eaten more quickly, however, corresponding to the upper limit of prey found in natural diets of most species.

DISCUSSION

Results of this study demonstrate that in spite of large differences in substrate use and differences in prey availability of those substrates, antwrens prefer to eat similar kinds of prey. Observations of wild and captive birds reveal a fundamental difference in the way these birds search for prey, however. Birds that normally forage on live foliage search directly for prey, selecting food from the array of available prey types. In contrast, dead-leaf foragers search for suitable substrates and then closely inspect these for hidden prey, taking prey roughly in proportion to what is available in the leaves. Dead-leaf specialists did not, however, exhibit a greater overall selectivity of prey, nor a greater tendency to avoid prey not normally encountered in nature. I conclude, therefore, that this specialization is achieved through a change in search behavior and is not accompanied by an equivalent change in prey preference.

Robinson and Holmes (1982) recognized the "substrate-restricted" searching mode, represented by the behavior of the Black-capped Chickadee (*Parus atricapillus*), as one of five foraging modes seen in insectivorous birds in a northern hardwoods forest. Chickadees, like the antwrens, searched specific substrates for hidden prey, but were opportunistic as to types of substrates searched. Greenberg (1987a) demonstrated that hand-raised Carolina Chickadees (*P. carolinensis*) exhibited exploratory behavior, but showed no consistent preference for particular substrate types. In contrast, hand-raised Worm-eating Warblers (*Helmitheros vermivorus*), a dead-leaf specialist in winter, showed an innate tendency to explore dead leaves more than other substrates. Greenberg (1987a) contrasted the presence of exploratory and manipulative behavior in species that normally search for hidden prey ("insurface" foraging) with the lack of such behavior in birds that forage on leaf surfaces. The antwrens I studied exhibited a similar contrast in degree of exploratory behavior associated with degree of insurface versus surface foraging. These behaviors may remain somewhat flexible to allow for short-term learning of local food abundances, as suggested by the temporary increase in dead-leaf searching behavior seen in the most generalized species, *hauxwelli*. Greenberg further demonstrated that behavioral plasticity in adult birds is related to degree of neophilia shown by juveniles in response to novel stimuli. Exploratory behaviors used in dead-leaf foraging might represent a neotenic retention of neophilia, which is usually extinguished by six to eight weeks of age (Greenberg 1987a).

Substrate-restricted foraging was associated with reduced diet breadth and greater stereotypy among individuals (low PDH), compared with the substrate generalist *hauxwelli*. However, dead- and live-leaf-foraging species were equally stereotyped, suggesting that both groups perceived their prey base as predictable. In this sense, both dead- and live-leaf-foraging birds may be considered evolutionarily specialized (Sherry 1990). The most consistent dietary difference between dead-leaf-specialist and other antwren species was the larger average prey size, and especially larger orthopterans, taken by the dead-leaf foragers. Because specialization on dead leaves imposes a cost in terms of lower foraging rates, and probably lower capture rates, compared with live-leaf foragers (Thiollay 1988, Rosenberg 1990a), the ability to take larger prey may be particularly important in these birds.

The maintenance of innate and highly stereotyped behaviors that restrict searching to one particular substrate must ultimately depend on the productivity of that substrate. Suspended dead leaves have been shown to be abundant in many tropical forest habitats, to support higher densities of arthropods than live foliage, and to be among the least seasonal of tropical forest resources (Greenberg 1987b, Boinski and Fowler 1989, Rosenberg 1990a, b). Comparisons of antwren diets and prey availability in my study further demonstrated that dead leaves provide a higher proportion of preferred prey types. The relative abundance of larger prey, especially large orthopterans, may be the single most important factor promoting specialization on dead leaves. Dead-leaf specialists, therefore, can search only these substrates with a high probability of finding acceptable prey and a low chance of encountering unsuitable prey (mainly ants). More generalized live-foliage searchers encounter a wider array of potential prey types and find a smaller proportion of these prey acceptable. That both specialists and generalists will eat a greater variety of prey in captivity than in the wild, however, suggests that natural diets are constrained by both availability and the ability of the birds to catch and handle certain prey. For example, antwrens probably rarely can catch butterflies, dragonflies, or lizards in the wild, but will eat them if given the opportunity. Thus, even substrate specialists maintain a degree of plasticity in terms of prey selection.

All species of antwrens studied preferentially selected orthopterans. Heavy predation on Orthoptera by tropical insectivores has previously been recognized as one of the fundamental differences between these species and insectivorous birds of the Temperate Zone, which eat primarily caterpillars during the breeding season (Greenberg 1981, Thiollay 1988). The diets of other dead-leaf specialists (mostly Furnariidae) contained large proportions of orthopterans (Rosenberg 1990a), as did the diets of four species of woodcreepers (Dendrocolaptidae;

Chapman and Rosenberg 1991), whereas other prey were more important to a guild of Neotropical flycatchers (Sherry 1984). Orthopterans were barely represented in the diets of temperate forest birds (e.g. Robinson and Holmes 1982), but grasshoppers (Acrididae) were important, at least seasonally, to species in shrub-steppe and desert riparian habitats (Rotenberry 1980, Rosenberg et al. 1982). Most identified orthopterans eaten by tropical species were katydids and crickets (suborder Ensifera), rather than Acrididae. Katydids and crickets tend to be soft-bodied, cryptically colored, and usually active nocturnally, while hiding motionless during the day (Belwood 1990). Acridids appear to be mostly diurnal, perching conspicuously and avoiding capture by jumping (pers. observ.). During feeding trials, both dead- and live-leaf-foraging antwrens reacted differently to these two kinds of orthopterans. Whereas nearly all ensiferans were quickly and eagerly consumed, acridids, which were often hard-bodied and brightly colored, tended to be ignored or eaten only after initial rejection. Several acridids, including a common species of spur-throated grasshopper (Cyrtacanthacridinae), obviously were distasteful to the birds; after initial attacks the birds would often bill wipe vigorously or show visible discomfort. Many of these insects were eventually eaten, however, without apparent ill effects. Antwrens also appeared to recognize or react to other prey as being distasteful. These included most stink-bugs (Pentatomidae), some caterpillars and butterflies, and all opiliones. These behaviors did not differ, however, between dead-leaf-specialist species and other species of antwrens.

Greenberg (1981) noted that tropical insectivores have longer and narrower bills than equivalent-sized temperate species, and attributed this difference to the efficiency of capturing the largest prey types in each region (orthopterans versus caterpillars). Besides being longer, antwren bills are considerably deeper (i.e. heavier) than those of small North American insectivores (e.g. Parulinae) and are distinctly hooked at the tip. Although Greenberg (1981) reasoned that longer bills are adaptive for capturing "highly mobile" orthopterans, the primary antipredator behavior of large katydids is to remain motionless and tightly grip the substrate (Belwood 1990, Rosenberg pers. observ.). During feeding trials, antwrens sometimes engaged in prolonged "tug-of-wars" with large katydids before successfully dislodging them from the substrates. I suspect, therefore, that the added depth (strength) of the bill, and especially the hooked tip, rather than the added length, enables these tropical birds to handle such large prey. Antwrens, and apparently all antbirds, rely entirely on the bill when manipulating and dismembering large prey. Some other birds, such as foliage-gleaners (*Automolus, Philydor*), greenlets (*Hylophilus*), and barbets (*Capito, Eubucco*), use the foot to hold prey against a branch while eating the prey (pers. observ.). This behavioral innovation greatly facilitates prey handling and reduces handling times. That captive antwrens would eat larger prey than those found in natural diets suggests that prey size may be limited more by handling time than by the physical capabilities of the birds. While manipulating and eating prey, these birds may be more vulnerable (i.e. more conspicuous and less vigilant) than during other foraging activities. Furthermore, long periods of prey handling causes birds to lag behind the mixed-species flocks in which they forage.

Although antwren species eat similar kinds of prey at gross taxonomic levels, it is likely that they overlap little in the species of arthropods that they encounter and eat. For example, katydids show species-specific preferences for diurnal roosting sites; individuals in dead and live leaves represent different species (Belwood 1990). The lack of greater taxonomic resolution in this and other dietary analyses may limit inferences that can be made about resource partitioning and potential competition. If, however, diet categories reflect both taxonomic and ecological similarities among prey (e.g. combining all larvae, separating roaches from other orthopterans), then further subdivision may add little information about predator-prey relationships (Cooper et al. 1990). Because antwrens do not appear to discriminate among subtle variations in their preferred prey types (e.g. brown versus green katydids), it is unlikely that specific coadaptations exist between particular bird and arthropod species. Furthermore, specialists were not more discriminatory than generalists, suggesting that limiting encounter to only a few prey species (those inhabiting dead leaves) does not necessarily influence criteria for prey choice.

Foraging experiments with caged birds have proven useful in studies of learning ability (e.g. Heinrich and Collins 1983, Greenberg 1984, 1987a), microhabitat patch use (Zach and Falls 1976), vigilance (e.g. Waite 1987), and prey-handling ability (e.g. Davies and Green 1976, Chai 1986), as well as prey discrimination and preference (e.g. Sherry and McDade 1982, Chai 1986, Greig-Smith 1987). These studies used both hand-reared and wild-caught birds, usually in a temporary aviary setting. Although it was not possible to maintain a captive population of antwrens in my study, these birds were excellent subjects for short-term experiments. Working with captive birds allowed me to distinguish between prey choice and response to prey availability, and provided the opportunity to observe and measure specific aspects of prey capture and handling not possible with only wild birds. The success of this approach may have been fortuitous, however, and may vary with the type of bird studied. For example, I attempted the same protocol with two individuals each of two other antbird species (*Hypocnemis cantator* and *Thamnomanes schistogynus*); none of these birds showed signs of adjusting to captivity, and none accepted any food in their cages. Whenever possible, however, experiments with wild birds, in combination with field data on prey availability and use, will enhance studies of foraging behavior and diet selection.

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