DIETS OF FOUR SYMPATRIC AMAZONIAN WOODCREEPERS (DENDROCOLAPTIDAE)[1]

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Abstract. Contents of 78 stomachs from four widespread and sympatric species of Amazonian woodcreepers (Dendrocolaptidae) were examined to assess the role of diet in resource partitioning. Orthopterans (25–35%) and beetles (10–32%) dominated the diets of all four species, despite large differences in foraging behavior. A higher proportion of spiders in the diet of *Dendrocincla merula* was associated with specialized ground-foraging at army ant swarms; however, specialization on dead leaves by *Xiphorhynchus guttatus* resulted in no significant dietary differences from the substrate generalist *X. spixii.* Overlap in diet was much greater than overlap in behavior for all species pairs, and the degree of diet specialization was unrelated to behavioral specialization. Taxonomic representation of prey in stomach contents differed significantly from field sampling of available prey in the three species tested, with orthopterans apparently selected by all species and beetles selected by *D. fuliginosa.* We suggest that behavioral differences may have evolved to reduce overt aggression (interference competition) but may not serve to reduce diffuse competition for food among syntopic species. Segregation in substrate use, however, may allow high diet overlap, suggesting a case of niche complementarity among these species.

Key words: Dendrocolaptidae; diet; foraging ecology; resource partitioning; specialization; woodcreepers; tropical forest birds.

INTRODUCTION

How large numbers of closely related species coexist in diverse tropical communities has intrigued ecologists for decades. Although studies of resource partitioning among potential avian competitors are numerous, studies that complement data on habitat selection and foraging behavior with data on diet are few (e.g., Rotenberry 1980, Robinson and Holmes 1982, Rosenberg et al. 1982, Dahlsten et al. 1985). This is especially true for species-rich tropical forest guilds; only Sherry (1984) has investigated the dietary relationships among sympatric neotropical insectivores, using 16 flycatcher species from Costa Rica.

The woodcreepers (Dendrocolaptidae) are a large and characteristic family of neotropical forest birds. Although superficially similar in external morphology and in their tendency to climb vertical trunks and branches, woodcreeper species exhibit a wide range of foraging behaviors. Many species typically join mixed-species foraging flocks in the understory or canopy (e.g.,

Munn 1985). Others follow swarms of army ants (*Eciton* spp.) to feed on escaping arthropods (Willis and Oniki 1978). In addition, many species do not feed directly on trunk or branch surfaces, but investigate clusters of dead leaves, vine-tangles, or palm fronds, or sally after flying prey (e.g., Pierpont 1986). The extent to which these behavioral differences may result in differences in diet is unknown.

Because up to 17 species of woodcreepers may coexist in parts of the Amazon Basin (e.g., Terborgh et al. 1984), their foraging relationships are a significant component of the overall community dynamics. In this paper, we describe the diets of four widespread species at two sites in southwestern Amazonia. We chose *Dendrocincla fuliginosa* (Plain-brown Woodcreeper), *D. merula* (White-chinned Woodcreeper), *Xiphorhynchus guttatus* (Buff-throated Woodcreeper), and *X. spixii* (Spix's Woodcreeper) because these were the most common large (>30 g) woodcreepers at each of these two well-sampled sites. Both species of *Dendrocincla* are "professional" followers of army-ant swarms throughout much of Amazonia (Willis 1972, 1979), although *D. fuliginosa* also forages away from ants. Both *Xiphorhynchus* spp. rarely follow army ants but routinely join mixed-species flocks in the understory and subcanopy (Munn 1985, Pierpont

1986; Rosenberg, unpubl. data). To address whether diet was important in niche partitioning by these species, we asked the following questions: (1) do differences in foraging behavior correspond to differences in diet? (2) do these species specialize on particular prey? and (3) how do species' diets relate to food availability?

METHODS

Diets were determined by direct observation of stomach contents from 78 individual birds: 32 *X. guttatus*, 18 *X. spixii*, 11 *D. fuliginosa*, and 17 *D. merula* (Table 1). Specimens were collected from June through August, mainly with mist nets, near Cobija, Dpto. Pando, extreme northwestern Bolivia, in 1986 (see Parker and Remsen 1987) and near Abujao, Dpto. Ucayali, eastern Peru, in 1987 by field parties from Louisiana State University Museum of Natural Science (LSUMNS). The two sites are in continuous, lowland rainforest, separated by roughly 200 km. Additional foraging and insect availability data were gathered at the Tambopata Reserve, Dpto. Madre de Dios, southeastern Peru, from 1987–1989.

Stomachs were preserved in 70% ethanol and housed permanently in the LSUMNS collection, along with reference skins or skeletons. Contents of each stomach were examined using a stereo-microscope (6–25×) with a micrometer. Because only a small number of items could be identified to family, most prey were identified to order or suborder, using Borror and White (1970), Borror et al. (1981), and Ralph et al. (1985). Prey items were sorted, measured, and counted, and sketches of identified material were made to facilitate later identification. Prey size was determined from measurable fragments using regression equations in Calver and Wooller (1982) or computed from arthropods collected in the study areas (Rosenberg, unpubl. data). Reference series of identified, mounted fragments, drawings, and photographs (Fig. 1) were prepared for future comparisons.

The question of differential digestion of hard- and soft-bodied prey is pertinent to any analysis of stomach contents (Rosenberg and Cooper 1990, and references therein). Hard-bodied items take longer to digest and may persist longer in the stomach. However, it seemed that the hard fragments of soft-bodied prey, such as orthopteran mandibles and spider fangs, were as prevalent in our samples as those of hard-bodied prey, such as beetles. We believe, therefore, that with knowledge of the particular fragments representing each food-type, we could detect hard- and soft-bodied prey equally well. Further experimentation would be needed to verify our impression.

The proportion of each prey category was determined separately for each stomach; diets were then determined as the average of the proportions in the individual stomachs of each species (i.e., samples were not pooled). Diet overlap between pairs of woodcreepers was calculated as: $O_a = \Sigma(P_{ia}P_{ja})/\sqrt{(\Sigma P^2_{ia})(\Sigma P^2_{ja})}$, where P_{ia} and P_{ja} are the proportions of prey category "a" in the diets of species "i" and "j" respectively (Pianka 1974, May 1975). Niche breadth, or prey-type diversity, was calculated for every stomach using $B = (\Sigma p_i^2)^{-1}$, where p_i is the proportion of taxon "i" in the stomach (Levins 1968). An average niche breadth was then calculated for each species. It is unclear whether pooled frequency distributions of prey items from multiple stomach samples can be compared statistically, because of potential pseudoreplication (Hurlbert 1984). Although in most cases individual arthropod prey captured by woodcreepers probably represent independent events (except for rare attacks on ant nests), we have conservatively chosen not to apply goodness-of-fit statistics to compare diets among species. We believe, however, that the patterns in dietary overlap are clear enough to indicate biologically significant trends, and our overall conclusions would not be altered.

For comparisons with the foraging behavior of these species, we drew upon data from several sources. First, woodcreepers were observed foraging as part of a general community study at the Bolivia study site and at the Tambopata Reserve in southeastern Peru (J. V. Remsen and Rosenberg, unpubl. data). These observations consisted of opportunistic sightings along forest trails, for each of which we recorded foraging height (estimated to the nearest 1 m), foraging substrate, perch site, prey-capture method, and an estimate of foliage density around the bird, as well as associated species (e.g., mixed-species flocks) and general habitat features. Data notation followed Remsen and Robinson (1990). Usually, fewer than five consecutive observations were made on each bird, although repeated sightings of (probably) the same individuals in the same mixed-species flocks were included. Because these efforts focused on mixed-species-
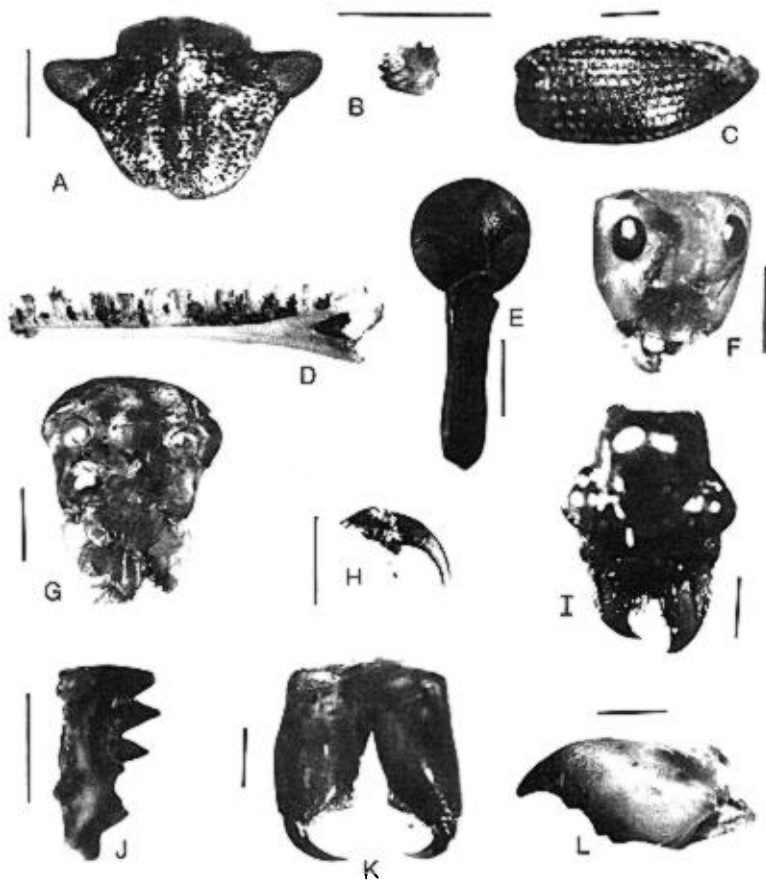
FIGURE 1. Fragmented prey items found in the stomachs of four woodcreeper species. A. Homoptera (head); B. Lepidoptera larva (mandible); C. Coleoptera (elytron); D. lizard (jaw); E. Curculionidae (head); F. ant (head with mandibles); G. roach (head with mandibles); H. spider (fang); I. Coleoptera (head with mandibles); J. Orthoptera (mandible part); K. spider (chelicerae with fangs); L. Orthoptera (mandible). Black bar indicates 1 mm.

flocking species, our samples are adequate only for the two *Xiphorhynchus* species. For the two species of *Dendrocincla*, we rely primarily on published accounts of their behavior in Willis (1972, 1979). Willis (1972) studied *D. fuliginosa* in lowland rainforest in Panama from 1960–1971 by observing behavior both at and away from army ants. Observations consisted of quantifications of behavioral characteristics, including height, diameter, and angle of perches, and substrates from which prey were taken. Willis (1979) used identical procedures to study *D. merula* in northern and eastern Brazil (Manaus, Belem) in 1973 and 1974. To compare these data with our observations of *Xiphorhynchus* spp., we calculated frequency distributions of foraging height and substrate use from Willis' published tables. Overlaps in substrate use among species were

then computed using the same procedure as for diets, based on the proportional use of seven categories common to all studies (see Fig. 7).

In these comparisons, we assume that geographic variation in each species' behavior throughout the lowland rainforests is considerably less than variation among the four species at our study sites. Although quantitative data on geographic variation are lacking, our observations suggest that these data sets represent the foraging roles of these four species in Bolivia and southern Peru. For example, *D. merula* is known to be an obligate army-ant follower throughout its range, and its behavior was found to vary little among 19 Amazonian study sites (Willis 1979); our few observations of this species were within 1 m of the ground at ant swarms. Our small sample of observations of *D. fuliginosa*, both at

TABLE 1. Characteristics of four Amazonian woodcreepers. Weights and measurements are averages of five male and five female specimens of each species at LSUMNS. Bill length is the exposed culmen; bill width measured at nares (both in mm).

Species	Body weight (g)	Bill length	Bill width	Number of stomachs	
				Peru	Bolivia
Dendrocincla merula	44.6	25.9	5.9	4	13
Dendrocincla fuliginosa	30.4	27.2	6.4	6	5
Xiphorhynchus spixii	36.4	32.3	5.6	13	5
Xiphorhynchus guttatus	57.8	38.3	6.1	19	13

and away from army ants, also is qualitatively similar to those of Willis in Panama (see Results).

We compared diets with data on prey availability for three of the four woodcreeper species. For the two ant-following *Dendrocincla* spp., we used data on arthropods flushed by army ants in Costa Rica (Otis et al. 1986). This study consisted of paired samples of leaf-litter plots before and after the passing of an ant swarm and also direct observations of arthropods fleeing the ants. We estimated prey availability to birds by combining counts of fleeing arthropods (from their Table 1) with the number of insects and spiders reduced on the paired plots. Other arthropods (e.g., isopods, ticks) found in the leaf-litter samples were not included because they were not observed fleeing from ants nor were they found in the diets of the woodcreepers. The diet of *X. guttatus* was compared with arthropods found in suspended dead leaves at the Bolivian study site (Rosenberg 1990). Samples consisted of 275 dead leaves, individually placed in zip-lock plastic bags and sprayed with insecticide; arthropods were then collected and later identified to lowest taxonomic level possible. No data were available on arthropods in the microhabitats used by *X. spixii*. These comparisons are necessarily crude, but they give a first approximation of the selectivity of prey items by these species.

RESULTS

DIET COMPOSITION

Diet composition within a species did not differ significantly between the two sites (*G*-test, all *P* > 0.06), except for *D. merula*, in which the Bolivian samples (*n* = 13) contained a greater proportion of spiders (24% vs. 10%) and fewer ants (9% vs. 31%) than those from Peru (*n* = 4). For further comparisons among species, data for both sites were pooled.

The majority (54–60%) of the diet of all four species consisted of Coleoptera and Orthoptera (Fig. 2). *D. merula* had the highest percentage of spiders (21%) and the lowest percentage of Coleoptera (10%). Spiders in the other three species ranged from 10–11% of total items in the diet. Ants were eaten consistently by all species except *D. fuliginosa*. Weevils (Curculionidae) were absent from *D. merula* but were particularly well represented in the two *Xiphorhynchus* species (33–50% of beetles). Minor prey items (1–10%) in all four species included roaches, lizards or frogs, bugs (Heteroptera), and insect larvae.

The four species overlapped considerably with respect to diet composition (Table 2). The greatest overlap was between *X. guttatus* and *X. spixii*, and the least was between *D. fuliginosa* and *D. merula*. *Dendrocincla merula* ate more soft-bodied spiders, roaches and orthopterans, whereas its congener preyed more on beetles and vertebrates. Overall dietary diversity was similar in these species, ranging from 4.8 in *D. merula* to 6.2 in *X. guttatus*, out of a possible 8.0.

To assess the adequacy of our samples, we examined the increase in the number of prey taxa represented in cumulative samples of randomly selected stomachs of each species (Fig. 3). In all species, the important arthropod orders and suborders considered in this study were represented after samples of only one to five stomachs. The additional prey taxa that accumulated in each species' diet included rare items such as earwigs, flies, scorpions, and centipedes, which together never exceeded 5% of the diet. To test further our sample sizes, we determined the number of stomachs necessary to estimate the proportion of each prey category within + or −0.05 of the total diet for each species at each site. In most samples, the cumulative estimates of diet composition was within 0.05 for all prey categories after five stomachs (Fig. 4). The exceptions were for ants in *X. guttatus* (up to eight stomachs needed) and in the small sample of *D. merula* from
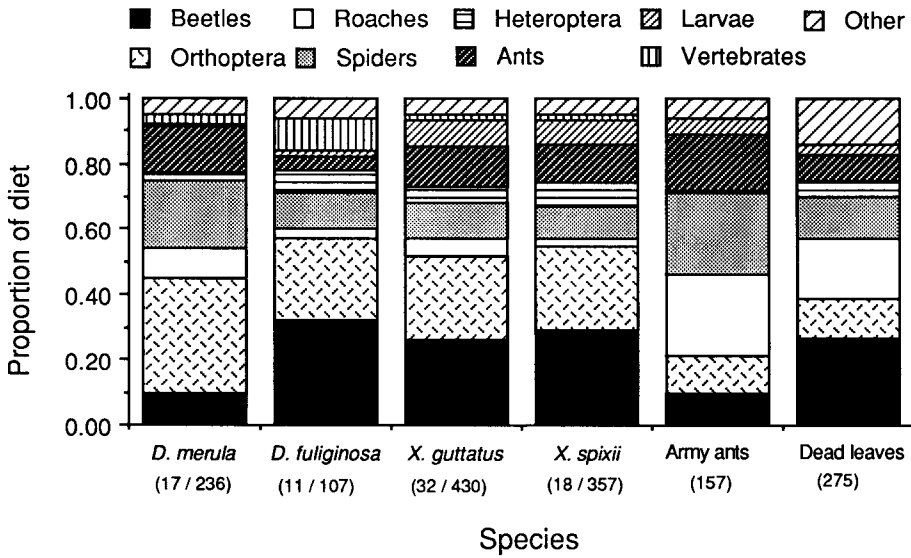
FIGURE 2. Diet composition of four woodcreeper species compared with prey flushed by army ants (data from Otis et al. 1986) and prey available in dead leaves. For bird species, numbers in parentheses are number of stomachs/number of prey items; for availability samples, number of arthropods.

Peru, in which total diet may not have been well represented. These results indicate low levels of individual variation in these species and suggest that our pooled samples of 10 or more stomachs for each species adequately represent their diets.

PREY SIZE

All four woodcreeper species ate a similar size range of the most important prey (Fig. 5), in spite of considerable differences among the woodcreepers in bill size and body weight (Table 1). *Dendrocincla merula* took, on average, slightly larger beetles and spiders than the other species, but none of the differences were significant (*t*-tests; all $P > 0.10$). The sizes of caterpillars, lizards, and other uncommon items could not be determined from digested fragments; however, they probably contributed little, if any, to differences in prey size among these species. In spite of substantial differences in bill length there was no relationship to prey size.

COMPARISON WITH FORAGING BEHAVIOR

In Brazil, *D. merula* perched usually within 1 m of the ground (Fig. 6), and about 90% of its foraging consisted of sallies to the ground in pursuit of arthropods fleeing the ants (Fig. 7; data from Willis 1979). At ant swarms in Panama, *D. fu-*

liginosa foraged as high as 10 m (Fig. 6) and sallied to trunks, vines, foliage, and air, as well as to the ground (Fig. 7; data from Willis 1972). At our study sites, *D. fuliginosa* was seen mostly from 5 to 8 m above ground (*n* = 34 observations), and it foraged from a variety of substrates including trunks (31%), air (31%), live foliage (23%), and epiphytes (8%). Therefore, the characterization of this species as an arboreal generalist, compared to the more restricted ground-foraging of *D. merula*, appears representative of their foraging at our study sites as well as those of Willis. In Peru and Bolivia, *X. guttatus* stayed mostly above 6 m (Fig. 6), and about two-thirds of its foraging was at suspended dead leaves, especially large *Cecropia* leaves and palm fronds (Fig. 7). *Xiphorhynchus spixii* foraged generally from 2 to 10 m above ground (Fig. 6), usually

TABLE 2. Dietary and behavioral overlaps among four woodcreeper species. Values above diagonal are for diet composition; values below diagonal are for substrate use. Equation for overlap given in text.

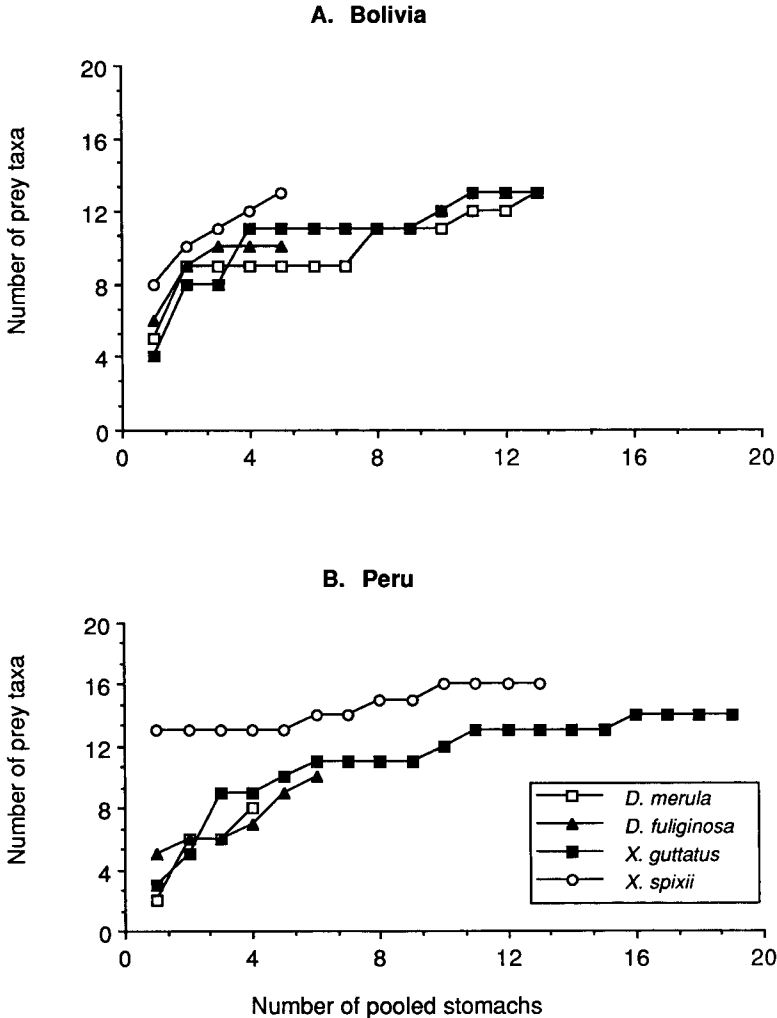|	*X. guttatus*	*X. spixii*	*D. fuliginosa*	*D. merula*
X. guttatus	—	0.999	0.986	0.906
X. spixii	0.419	—	0.957	0.830
D. fuliginosa	0.196	0.649	—	0.780
D. merula	0.017	0.034	0.444	—

A. Bolivia

B. Peru

FIGURE 3.   Number of prey taxa in cumulative samples of stomachs from four woodcreeper species at two sites.

pecking at trunks or probing under vine stems or epiphytic moss and lichens (Fig. 7).

The overlap in diets among these four species in all cases was much greater than their overlap in foraging substrate use (Table 2). In the two ant-following species, almost total segregation in foraging height and substrate use may have resulted in a shift in the proportions of main prey categories, with more spiders and roaches in the diet associated with the ground-foraging *D. merula* and more beetles associated with foraging on trunks and vines in *D. fuliginosa*. *Xiphorhynchus guttatus,* which forages often on suspended dead leaves, had a noticeably different diet, at least in terms of prey orders, from *D. merula* and *D. fuliginosa* but was nearly identical to *X. spixii.*

Diversity of feeding behaviors was not consistently related to diet diversity. *Dendrocincla merula,* with the most restricted mode of foraging, also had the least diverse diet, whereas the somewhat specialized *X. guttatus* had a slightly more diverse diet than *X. spixii.*

PREY AVAILABILITY

Based on the behavioral summary above, we were able to compare the diets of three species with data on prey availability. Arthropod prey displaced by army ants in Costa Rica (Otis et al.
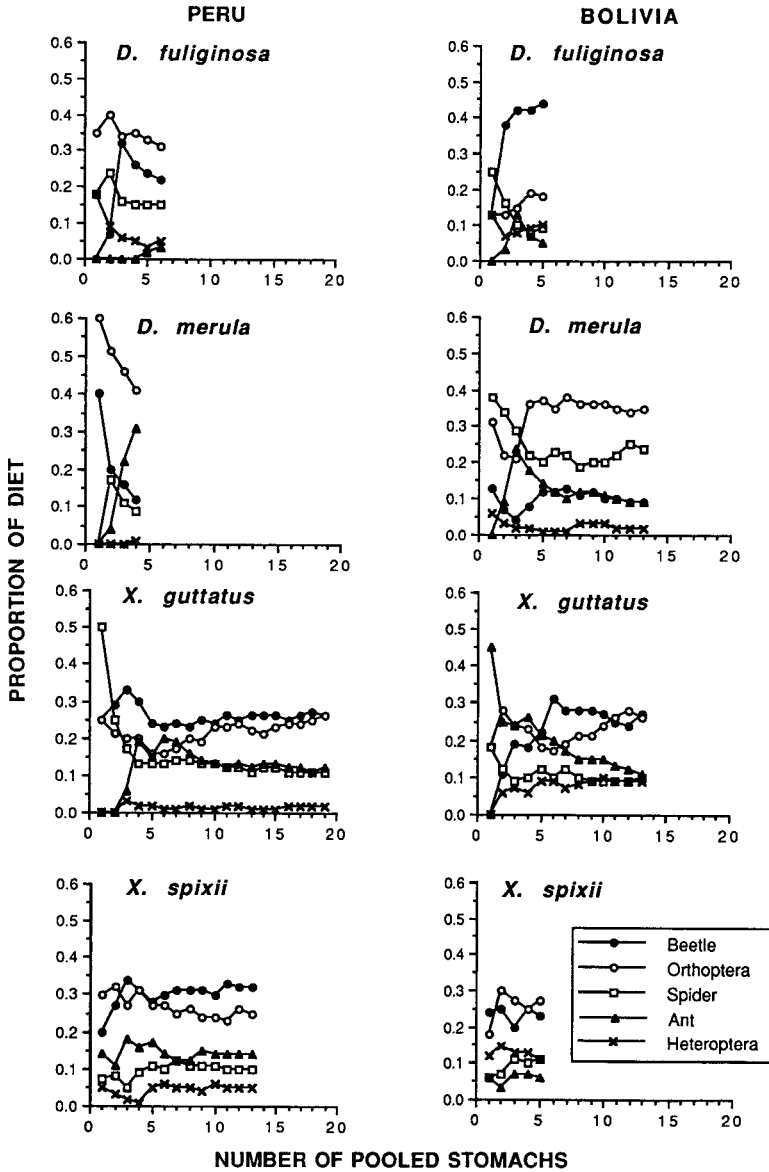
FIGURE 4.   Proportions of prey taxa in cumulative samples of stomachs for four woodcreeper species at two sites.

1986) consisted mainly of spiders, roaches, and ants, whereas prey available in suspended dead leaves consisted of beetles, roaches, spiders, and orthopterans (Fig. 2). In all comparisons, the woodcreepers' diets were different from the distributions of available prey. The ant-following *D. merula* appeared to select orthopterans and avoided small roaches, but took other prey approximately in proportion (+ or − 10%) to that flushed by army ants (Fig. 8). *D. fuliginosa* ate

more beetles and orthopterans than expected and fewer roaches, spiders, and ants. In comparison with prey availability in dead leaves, *X. guttatus* ate slightly more orthopterans and fewer roaches; all other prey were eaten in proportion to their availability.

DISCUSSION

In this study we have documented dietary differences in four woodcreepers with different for-

A. Beetles
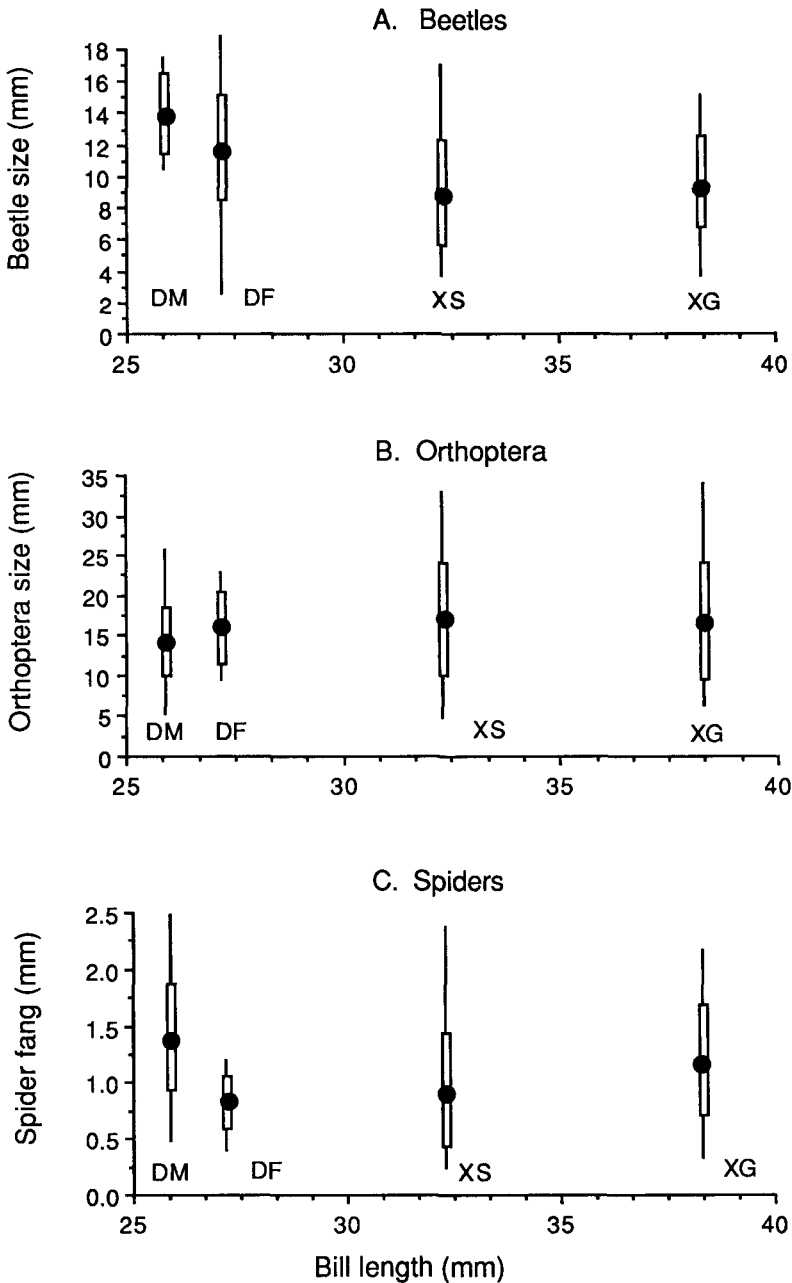

B. Orthoptera

C. Spiders

FIGURE 5. Comparison of bill length with prey size in four woodcreeper species. Bars indicate one standard deviation; vertical lines indicate range. DM = *Dendrocincla merula,* DF = *D. fuliginosa,* XS = *Xiphorhynchus spixii,* XG = *X. guttatus.*

aging habits. Although some differences in diet were detected, they nonetheless represent only subtle shifts in the proportions of major prey types. Dietary overlap was high for most species-pairs, and all species were more similar in diet than in foraging behavior.

Dendrocincla merula and *D. fuliginosa* compete for food at ant swarms (Willis 1979). *D. merula* is usually dominant, occupying the center of the swarm, close to the ground, where prey is most abundant. *D. merula* also is less adept at arboreal foraging, with less stiffened rectrices than
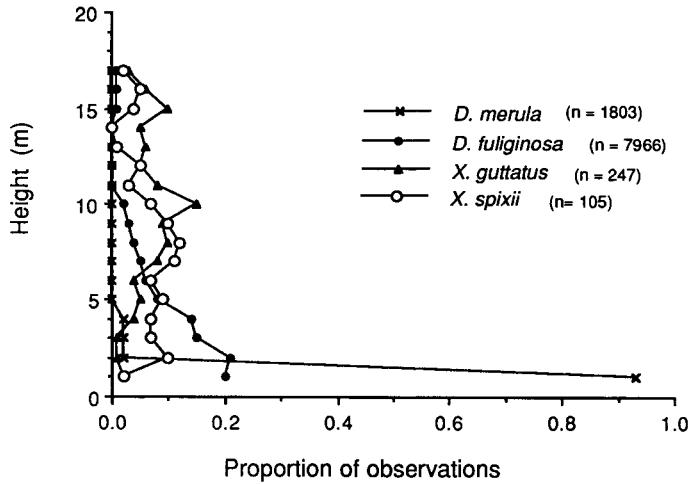
FIGURE 6.   Foraging heights of four woodcreeper species. Data for *D. merula* from Willis (1979); data for *D. fuliginosa* from Willis (1972); data for *X. guttatus* and *X. spixii* from this study.

other woodcreepers and more "clumsy" sallies to substrates above the ground (Willis 1979). Thus, the behavioral differences and consequent dietary shifts between the two *Dendrocincla* are actively maintained by a dominance hierarchy at their shared foraging sites. The diet of *D. merula* was more similar to our estimate of prey availability at ant swarms than was that of *D. fuliginosa*. This difference, and especially the large number of beetles eaten by *D. fuliginosa,* may relate to increased foraging away from army ants by this species. Pierpont (1986) considered both

Dendrocincla spp. to be members of a sallying guild of woodcreepers at Manu National Park, Peru. She found *D. merula* to forage more frequently above the ground at palms and dead leaves, where it takes flushed prey normally hidden inside these substrates. Foraging of *D. fuliginosa* was more restricted to trunks and vine surfaces, and less often at ants.

Willis (1972, 1979) rarely observed *Dendrocincla* spp. preying on beetles, although 30–42% of the observed prey in those studies (especially small prey) were not identifiable. The small num-
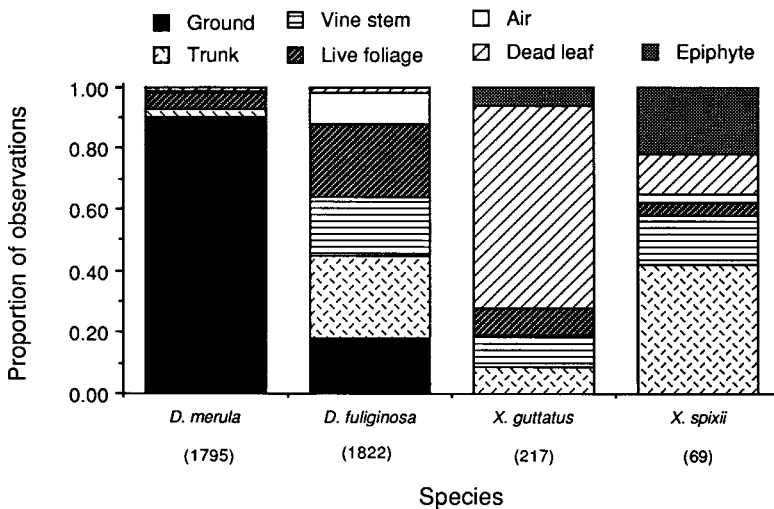

FIGURE 7.   Foraging substrate use by four woodcreeper species. Samples sizes in parentheses are number of observations. Data sources same as Figure 6.
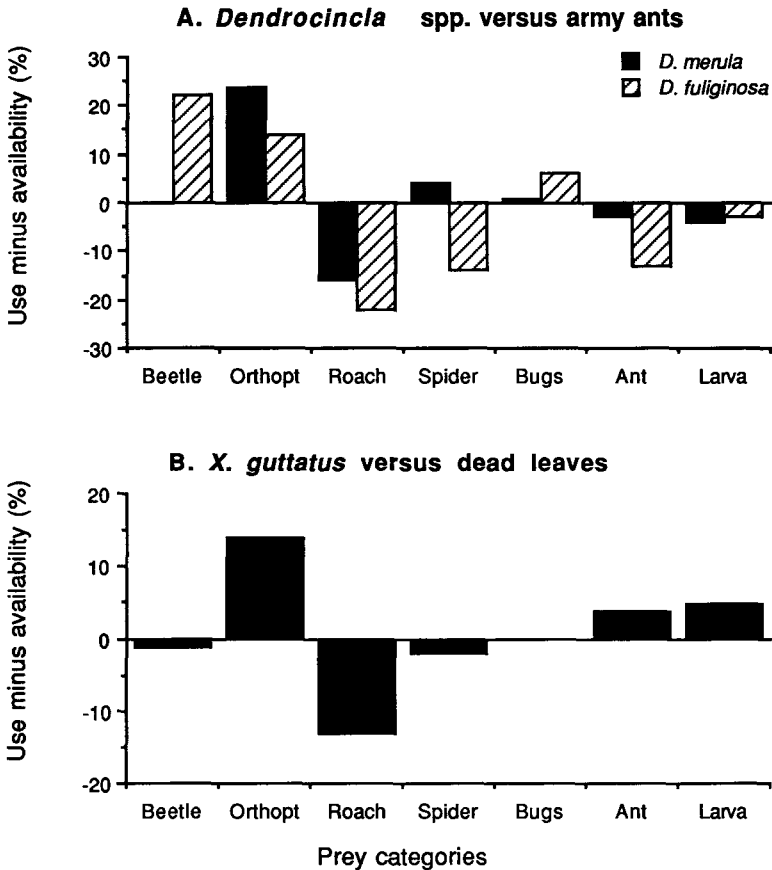
FIGURE 8. Comparison of diet and prey availability for three woodcreeper species. Horizontal mid-line indicates use equal to availability; bars above and below horizontal represent prey categories selected or avoided, respectively. A. *D. merula* and *D. fuliginosa* compared with arthropods flushed by army ants (Otis et al. 1986); B. *X. guttatus* compared with arthropods in dead leaves in Pando, Bolivia.

ber of beetles seen at an army-ant swarm by Otis et al. (1986) also may not reflect their true availability to woodcreepers. Data from leaf-litter traps in the same area showed that beetles made up about 12% of the arthropod fauna (Otis et al. 1986), and Pearson and Derr (1986) found that beetles made up 13% of the litter arthropods in *terra firme* forest in Peru.

In the mixed-species flocks in which *Xiphorhynchus* woodcreepers forage, overt aggression between *X. guttatus* and *X. spixii* is rare (Pierpont 1986), and competition for food, if present, is diffuse. *Xiphorhynchus guttatus* and *X. spixii* do not avoid flocks in which the other species is present. Of 91 mixed-species flocks censused by Rosenberg in Peru, 36 had *X. guttatus,* 14 had *X. spixii,* and 7 had both species; i.e., these species were distributed independently among flocks

($x^2 = 0.30$, ns). Although these two species differed in substrates searched for food, overlap in their diets was nearly complete. *Xiphorhynchus guttatus* might be expected to compete more directly with other large-bodied flock members that search dead leaves, such as foliage-gleaners (*Automolus* and *Philydor* spp.) and barbets (*Eubucco* spp.). These various species will occasionally search the same clusters of dead leaves without exhibiting overt aggression (Rosenberg 1990), although Pierpont (1986) observed several displacements of foliage-gleaners by *X. guttatus.* However, diet composition of *X. guttatus* overlapped more with the other arboreal woodcreepers (*X. spixii* and *D. fuliginosa*) than with any dead-leaf foraging species (Rosenberg 1990). Furthermore, *X. guttatus* ate smaller prey, especially smaller orthopterans, than most of the

dead-leaf foraging species, overlapping most in prey size with the much smaller *Myrmotherula* antwrens (Rosenberg 1990).

Compared with birds in temperate communities, tropical birds are generally thought to be more specialized, in association with greater species-packing and more finely divisible resources (e.g., Orians 1969, Terborgh 1980). Several levels of specialization may occur, as seen in the four woodcreepers studied. In none of these cases, however, did specialized behaviors result in a specialized diet. Sherry (1990) has argued that foraging specialization may result in stereotyped, but not necessarily narrow, diets. The low intra-population variability in diets seen in these species suggests that the woodcreepers are evolutionary (strategic) specialists, yet may be ecological (tactical) generalists (sensu Sherry 1990).

Why then did these various behaviors evolve if these species continue to exploit a broadly similar resource base? First, it is possible that similar morphology and reliance on vertical perches constrains the diets of these woodcreepers to be similar. Second, it is possible that behavioral modifications evolved largely as a means of avoiding physical interactions with other species while foraging, thus reducing interference competition (Pierpont 1986) but not diffuse competition for food. Finally, it is likely that these species are taking different prey, but our level of prey identification could not detect these differences. For example, beetles in the family Curculionidae were prevalent in diets of *Xiphorhynchus* species but not in *Dendrocincla* species.

Because these woodcreepers differ in their use of substrates and foraging space, high overlap in diet is perhaps not unexpected. This may represent a case of complementarity of niches, with segregation in use of substrates being sufficient to allow similar diets. However, other dead-leaf foraging species, which overlap greatly in substrate use, also overlap broadly in composition of their diets (Rosenberg 1990). Until we understand more precisely the dietary relationships of other species in these diverse communities, as well as the distribution of prey among foraging substrates, the role of foraging specialization in maintaining high species richness will remain vague.

ACKNOWLEDGMENTS

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