Ornithological Monographs
Volume 48 (1997), pp. 445–483

INSIGHTS INTO THE MAINTENANCE OF HIGH SPECIES DIVERSITY IN THE NEOTROPICS: HABITAT SELECTION AND FORAGING BEHAVIOR IN UNDERSTORY BIRDS OF TROPICAL AND TEMPERATE FORESTS

PETER P. MARRA[1] AND J. V. REMSEN, JR.
Museum of Natural Science, Foster Hall 119, Louisiana State University,
Baton Rouge, Louisiana 70803, USA;
[1]present address: Department of Biology, Dartmouth College,
Hanover, New Hampshire 03755, USA

ABSTRACT.—For almost three decades, structural habitat complexity has been regarded as a primary ecological factor responsible for maintaining high species diversity of tropical bird communities. However, differences in habitat complexity between temperate and tropical forests have not been documented sufficiently. Differences between temperate and tropical forests were quantified by measuring 36 variables related to understory habitat structure. Structural components of temperate and tropical habitats differed significantly in several features. However, no differences were found in overall habitat heterogeneity (i.e. complexity) between temperate and tropical forests. To search for "bird-related" factors important in maintaining high tropical species diversity, we compared habitat selection between foliage-gleaning insectivorous birds in temperate and tropical forest understories. The tropical species were more specialized in horizontal and vertical habitat selection, and had lower "niche breadths" in foraging substrate and in foraging height. Tropical species also showed less interspecific overlap in most foraging variables than did temperate species. Therefore, higher species diversity, at least within this guild of birds in tropical and temperate forest understories, can be attributed at the proximate level to greater specialization and "tighter species packing," and may be more independent of greater habitat complexity than previously thought.

RESUMEN.—Por casi tres decadas, la complejidad estructural del habitat se ha considerado como el principal factor ecologico responsable de mantener la alta variedad de especies encontrada en comunidades de pajaros tropicales. Sin embargo, la diferencia en complejidad del habitat entre bosques templados y bosques tropicales no ha sido suficientemente quantificada. Nosotros quantificamos diferencias entre bosques templados y bosques tropicales midiendo 36 variables relacionadas a la estructura del habitat bajo el dosel y encontramos varias diferencias significativas en componentes estructurales entre habitats tropicales y templados. Sin embargo, no encontramos diferencias en la heterogeneidad del habitat (complejidad) entre bosques templados y tropicales. Buscando factores que fueran importantes en mantener la alta diversidad de las especies de pajaros tropicales, comparamos la seleccion del habitat entre pajaros insectivoros que usan el follaje bajo el dosel en bosques templados y tropicales. Las especies tropicales estaban mas especializadas en su seleccion de habitats al nivel horizontal y vertical, teniendo pequenos nichos en el substrato y altitud del area donde forrajeaban. En la mayoria de las variables relacionadas al forraje, las especies tropicales tambien demonstraron menos traslapo entre-especies que las especies templadas. Concluimos pues que la alta variedad de especies, por lo menos dentro de este grupo de pajaros que viven bajo el dosel en bosques templados y tropicales, se puede atribuir inicialmente a mayor especializacion y concentracion de especies y puede que sea mas independiente de la total complejidad del habitat de lo que actualmente se cree.

Why tropical rainforests, particularly those of South America, harbor the greatest number of bird species in the world is a question that continues to intrigue ornithologists. The striking difference in species richness stimulates such intrigue: over 300 species of resident forest birds can be found in an area of about 3 km^2 of Amazonian rainforest (Terborgh et al. 1984), whereas in a comparable area of temperate forest, no more than 50 species typically coexist (and usually no more than 30). As many as 40 species in a single family, the antbirds (Formicariidae), can be found at a single Amazonian forest site (e.g., Terborgh et al. 1984); thus, single-site species richness of one family alone may exceed that of all forest birds combined at many temperate localities. No consensus exists concerning explanations of high species richness of the tropics because the answer involves complex interactions among ecological and historical factors; such factors, at the ultimate level of causation, are intrinsically difficult to investigate.

Testing hypotheses concerning proximate causes of diversity, or factors that maintain diversity, however, is potentially more feasible, as outlined by Remsen (1990). Three hypotheses have been proposed to explain single-point (alpha) diversity at the proximate level in tropical forests: (1) *Increased Resource Diversity*—This hypothesis suggests that more species are able to coexist because of greater resource diversity in the tropics, such as greater structural habitat complexity (MacArthur and MacArthur 1961; MacArthur et al. 1962; MacArthur 1969; Orians 1969; Karr 1971; Willson 1974; Cody 1975; Terborgh 1980a) or unique tropical resources such as bamboo (Parker 1982; Kratter 1995, and in press) or dead leaves suspended in vegetation (Remsen and Parker 1984; K. Rosenberg 1990 1997); (2) *Increased Specialization*—This hypothesis proposes that species are more specialized in the tropics, and therefore more species can "pack" into available habitats (Klopfer and MacArthur 1960); (3) *Increased Ecological Overlap*—This hypothesis proposes that there is greater niche overlap among tropical species, permitting more species to coexist in a given area (Klopfer and MacArthur 1961; May and MacArthur 1972).

These hypotheses are not mutually exclusive, and they all predict a direct causal relationship between diversity and resource use. In this study we tested these three hypotheses by comparing (1) structural habitat complexity and (2) the specificity of macrohabitat, microhabitat, and foraging site selection between a similar guild of tropical and temperate zone birds.

Despite the obvious need for comparative data on habitat selection in tropical and temperate bird species, few data are available. By habitat selection, we mean comparing habitat availability to habitat use by birds. So far, research quantifying habitat preference in tropical birds has consisted only of describing habitat use at the macrohabitat scale by comparing species composition among different habitats or forest types (e.g., Orians 1969; Terborgh and Weske 1969; Karr 1971; Willson et al.. 1973; Karr and Freemark 1983; Lovejoy 1974; Remsen and Parker 1983; Terborgh et al. 1984; Terborgh 1985; De Visscher 1984; Willson and Moriarty 1976; Silva and Constantino 1988; Thiollay 1988a; G. Rosenberg 1990) or at the scale of foraging substrates within a habitat (e.g., Stiles 1978; Askins 1983; Remsen 1985; Thiollay 1988b; K. Rosenberg 1990).

With few exceptions, studies that have quantified microhabitat selection within a forest habitat have been restricted to the temperate zone (e.g., James et al. 1984; Cody 1985; Morse 1985). The exceptions (Kikkawa et al. 1980; Schemske and Brokaw 1981; Karr and Freemark 1983; Wunderle et al. 1987; Levey 1988) relied exclusively on mist-net capture data. We believe that the use of mist nets for determining microhabitat selection of birds is unsound. General problems in interpreting data from mist-net captures have been discussed elsewhere (Karr 1971, 1981; Lovejoy 1974; Remsen and Parker 1983; Terborgh 1985; Remsen and Good 1996). Specifically with respect to microhabitat selection, mist-net data have the following problems: (1) Capture in a mist net means only that the bird was *flying through* that air space, not necessarily that it was using the microhabitat near the mist net (Remsen and Good 1996). In fact, there might be an inverse relationship between use of microhabitat within a few meters of the net and likelihood of capture, because those individuals foraging in the vegetation near the net are probably more likely to detect the net than are those only passing through in flight. This problem is particularly severe for those species with mobile spacing systems, nonterritorial social systems, or relatively large distances between foraging sites, which make them especially prone to mist-net capture (Remsen and Parker 1983; Remsen and Good 1996), e.g., *Pipra* spp., *Manacus* spp., *Mionectes* spp., *Phaethornis* spp., *Glyphorynchus spirurus*, dead-leaf-searching specialists such as certain *Myrmotherula* spp. and *Automolus* spp., and ant-following antbirds such as *Pithys albifrons*, *Hylophylax* spp., *Phlegopsis* spp., and *Rhegmatorhina* spp. (2) Probability of capture in a mist net varies with mist net placement, vegetation density, and incidence of light. For example, a species might actually prefer a certain habitat but would be unlikely to be captured there because the net is more easily detected where vegetation density is low or sunlight frequently exposes the net. (3) Few species of forest undergrowth birds are completely restricted to the first 2–3 m above ground that is the upper limit sampled by mist nets; whenever undergrowth species use microhabitat higher than 2–3 m, this use is "invisible" to mist-net sampling.

In addition to the problems of using mist net data, previous studies have not included detailed habitat measurements to determine habitat availability. Typically, habitat structure has been measured solely by foliage-height-diversity (FHD) profiles (MacArthur and MacArthur 1961), and a species' habitat use has been quantified only with respect to the vertical range within a FHD profile. Although a general relationship between FHD profiles and avian species diversity exists, it is not able to account for differences in species diversity among tropical areas with similar FHD profiles (Orians 1969; Pearson 1975) or similar bird diversities among tropical areas with very different FHD profiles (Terborgh and Weske 1969). Moreover, FHD profiles do not measure specific structural features that might be critical to bird species diversity (Lovejoy 1974). We are not aware of any studies that have compared habitat use to habitat availability at the "horizontal" level. Studies of habitat selection by tropical birds using actual observations rather than mist-netting, combined with detailed information on habitat availability, are nonexistent.

We compared habitat selection between temperate and tropical forest birds using standard methods at both sites and by studying a group of ecologically similar species, namely understory foliage-gleaning insectivores. Because precise counterparts are naturally difficult to identify, we focused on the most common species in this guild at our temperate and tropical sites. By choosing only the most common species, we are unable to determine whether our results are biased by lack of data on the uncommon species. Although between-biome comparisons involving phylogenetically unrelated organisms can be inappropriate because of uncontrollable variables, these problems are inherent and unavoidable. Nevertheless, we regard our approach as a logical first step.

METHODS

Our temperate zone study site was at the Tensas River National Wildlife Refuge (hereafter Tensas), in Madison, Franklin, and Tensas parishes (32°12'N, 91°25'W), northeastern Louisiana. The refuge contains approximately 40,500 ha of bottomland hardwood forest and as such is one of the largest tracts of relatively undisturbed deciduous forests remaining in the southeastern United States. Data were collected from 22 May to 3 June 1988.

Our study area, known locally as Fairfield Woods, is considered "high floodplain" forest. Little, or no standing water was present on the study site while data were collected. The forest is dominated by sweetgum (*Liquidambar styraciflora*) and willow oak (*Quercus phellos*); also present are overcup oak (*Quercus lyrata*), water hickory (*Carya aquatica*), cedar elm (*Ulmus crassifolia*), red maple (*Acer rubrum*), and bald cypress (*Taxodium distichum*). The primary understory vegetation consists of greenbriar (*Smilax*), swamp palmetto (*Sabal minor*), and common buttonbush (*Cephalanthus occidentalis*) (Barrow 1990).

The tropical forest study site was at the Tambopata Reserved Zone (hereafter Tambopata), southeastern Peru, approximately 30 km southwest of Puerto Maldonado on the south bank of the Río Tambopata, depto. Madre de Dios (12°50'S, 69°17'W). Data were collected from 25 June to 7 August 1988.

The biota of this 5,500-ha. reserve is among the richest in the world. So far, 550 species of birds have been recorded since 1977 (Foster et al. 1994), whereas only 244 species have been recorded on the temperate study site (R. B. Hamilton, unpubl. data). At Tambopata on a 1.0-ha plot, 153 species of trees represented by individuals 10 cm or more in diameter at breast height (DBH) were recorded (G. Hartshorn pers comm. in Parker 1982). In contrast, only 26 species of trees have been recorded in all of Tensas N.W.R. (Barrow 1990). For more details on the reserve and its habitats, see Parker (1982) and Erwin (1984).

At Tambopata, data were collected in three forest types (following Remsen and Parker 1983): (1) river-edge forest, (2) transitional forest, and (3) *terra firme* forest. Below we give a brief qualitative description of these forest types; for a more thorough and quantitative analysis see Marra (1989).

Because of annual or historical disturbance by river action, river-edge forest has a more open canopy, allowing for more light penetration and consequently a denser forest understory. Large, almost impenetrable thickets of *Heliconia* spp. and bamboo (*Guadua* sp.) were common. Two km of trail and adjacent forest formed our river-edge forest site. Although the river mostly parallels the trail, our study site did not include the riverbank itself.

The second forest type, "transitional forest," was studied along 3.6 km of trails and adjacent forest. Transitional forest is poorly drained, low-lying forest with occasional knolls or small hills. It is flooded seasonally by rainfall or by rain-swollen streams. Transitional forest differs most importantly from river-edge forest in its more continuous and taller canopy. Bamboo thickets and *Heliconia* spp. were present in this habitat, but to a much lesser degree than in river-edge forest.

TABLE 1

STUDY SPECIES IN TEMPERATE AND TROPICAL FORESTS

Scientific name (abbreviation)	English name
TEMPERATE SPECIES	
Cardinalis cardinalis (Cc)	Northern Cardinal
Thryothorus ludovicianus (Tl)	Carolina Wren
Vireo griseus (Vg)	White-eyed Vireo
Wilsonia citrina (Wc)	Wilson's Warbler
Oporornis formosus (Of)	Kentucky Warbler
TROPICAL SPECIES	
Myrmoborus myotherinus (Mm)	Black-faced Antbird
Myrmoborus leucophrys (Ml)	White-browed Antbird
Formicarius analis (Fa)	Black-faced Antthrush
Formicarius colma (Fc)	Rufous-capped Antthrush
Myrmeciza hemimelaena (Mh)	Chestnut-tailed Antbird
Hypocnemis cantator (Hc)	Warbling Antbird
Corythopis torquata (Ct)	Ringed Antpipit

The third forest type, *terra firme* forest, is on slightly higher ground and is not flooded. Two km of trail and adjacent forest formed our study area in this habitat type. Only an occasional sprig of bamboo or small patch of *Heliconia* was present.

The target birds at Tambopata (Table 1) were six species of understory antbirds (Formicariidae) and one understory flycatcher (Tyrannidae); all seven species are common, widespread species in Amazonia. They were selected because they were fairly common at the sites and relatively easy to find and follow. To minimize the influence of social factors on habitat selection, none of the seven target species was an army-ant-follower or member of mixed-species flocks; individuals forage predominantly alone, in pairs, or in small family groups. To minimize the direct influence of plant resources on habitat selection (Terborgh 1985), only insectivores were chosen (vs. frugivores or nectarivores). Species chosen for comparison from the temperate zone differ phylogenetically from the tropical species, but are ecologically similar in being common passerine insectivores of forest undergrowth (Table 1).

To quantify habitat availability, and to compare vegetation heterogeneity within tropical and between tropical and temperate forests, 36 variables were measured at the tropical study sites and 32 at the temperate study site (Table 2). A total of 200 random samples was taken at the temperate forest site and 204 at the tropical site (80 in river-edge forest, 144 in transitional forest, and 80 in *terra firme* forest). At each sample point, variables were quantified in two concentric, cylindrical plots, 2 m and 10 m in diameter, extending from the ground to 5 m above the forest floor. This technique was first developed by Moser et al. (1990) and was modified for this study. Only three variables were not shared between temperate and tropical sites (Table 2): bamboo, *Heliconia,* and palms were unique to the tropical sites, and palmetto was unique to the temperate site.

The target bird species were censused at Tambopata to determine habitat preferences at the macrohabitat level (river-edge, transitional, or *terra firme* forest). Censuses began at sunrise and lasted approximately 1 hr. Three censuses were conducted in river-edge, five in transitional, and five in *terra firme* forest. All singing individuals (as well as individuals seen at other times of the day) within 50 m to either side of the trail were spot-mapped and considered to represent one pair. Final relative abundance estimates (pairs per km of trail) were based on the maximum number of pairs seen in each forest type. To assess the relative abundances of the target species at the temperate forest site, the total number of pairs seen or heard was estimated daily. By the end of the study at Tensas, Marra was familiar with the territories of all target species within the study site and was able to estimate the number of individuals of each target species.

For data on habitat use and foraging, birds were located by either sight or sound, more typically by the latter in the tropics. Upon locating a bird, it was watched until a prey attack was seen. The exact point of the attack was used as the center point of the 2-m and 10-m-cylinders (modified after Moser et al.. 1988). A minimum of 60 s elapsed between marking of foraging points. A maximum of five foraging points was flagged for any one individual in a given day. The tropical species were extremely difficult to find and observe, so when an indi-

TABLE 2

DESCRIPTION OF VARIABLES AND MEASUREMENT TECHNIQUES

Canopy Height (CH)	Rangefinder; measurement taken directly above foraging point or random sample point.
Percent Canopy Cover (CC)	Spherical densiometer (Lemmon 1956, 1957). Measurement taken directly above foraging point or random sample point.
Gap Association	Frequency of gap occurrence within 10-m cylinder. A gap is considered any open area in understory larger than 3 m in diameter or an area where large amounts of sunlight penetrate below the 2-m ceiling of the 10-m cylinder in the undergrowth (modified after Brokaw 1982). Classified as: (a) Artificial—manmade (i.e. trail) or (b) Natural—treefall; or bamboo.
% Ground Cover (GC)	Estimate (2- and 10-m) of all foliage 0–30 cm above ground.
% Shrub Cover (SC)	Estimate (2- and 10-m) of all shrub foliage 30 cm–3 m
Stems	Counts of stems in 2- and 10-m cylinders.
Fallen Logs (FL)	Counts of fallen logs in 2- and 10-m cylinders.
Mean Leaf-litter (LL)	Mean number of leaves on ground at five point-samples in both 2- and 10-m cylinders.
% Volume Vines (VV)	Estimate of vine volume from total composition in 2- and 10-m cylinders.
% Volume Palms (VP)	Estimate of palm tree volume from total composition in 2- and 10-m cylinders (tropics only).
% Volume Palmetto (VP)	Estimate of palmetto volume from total composition in 2- and 10-m cylinders (temperate only).
% Volume Bamboo	Estimate of bamboo volume from total composition in 2- and 10-m cylinders (tropics only).
% Volume Heliconia	Estimate of *Heliconia* volume from total composition in 2- and 10-m cylinders (tropics only).
% Suspended Dead Leaves	Estimate of suspended-dead-leaf volume from total composition in 2-m cylinder.
% Dead Stems	Estimate of dead-stem volume from total composition in 2-m cylinder.
% Live Leaves	Estimate of suspended live-leaf volume from total composition in 2-m cylinder.
% Live Stems	Estimate of live-stem volume from total composition in 2-m cylinder.
% Air Space	Estimate of open-space availability in 2-m cylinder.

vidual was found, it was necessary to maximize the number observations. If a bird seemed disturbed or altered its behavior, observations were not taken on that individual. To avoid biasing the data in favor of readily observed individuals, no more than 10 observations were taken on an individual bird or pair during the study period, although without color-banded individuals we could not be sure. In both localities, the size of the study sites was large enough to include many pairs.

Three foraging-site variables were recorded at each observation: foraging maneuver, foraging substrate, and foraging height following the terminology of Remsen and Robinson (1990). Each foraging substrate was classified as one of the following: live leaf, dead leaf, live stem, dead stem, vine, palm, palmetto, leaf litter, bare ground, bamboo stem, bamboo leaf, bark, spider web, or air. Heights of foraging observations were measured either with a meter tape or, for foraging points higher than 3 m, a range-finder.

Data analysis.—Rotated orthogonal and nonrotated factor analyses were performed to identify patterns and search for multicolinearity among variables for each habitat type (SAS 1982). To assess overall habitat heterogeneity, general variances were calculated for each forest type. The general variance is the determinant of the variance-covariance matrix computed from the measured variables in each habitat type. It provides a way of consolidating the information on all variances and covariances into a single number (Johnson and Wichern 1982). The general variance is calculated by summing the products of the covariances and subtracting the products of the variances (Johnson and Wichern 1982; SAS Institute 1985). The final value for the general variance is reported as the natural log of the calculated determinant from each matrix. To determine whether a bird species was preferring or avoiding a particular type of microhabitat (as measured by our microhabitat variables; Table 2), we compared the frequency distributions of a bird species' use of a particular variable (as measured by our observational data) with that variable's availability (as measured by our random microhabitat sampling). If these frequency distributions differed significantly (Kolmogorov-Smirnoff tests, $P \leq .05$), we classified species to be preferring (i.e., selecting) or avoiding that microhabitat variable.

To determine the degree of specialization in foraging, niche breadths were calculated for each species in each habitat type using the formula:

$$B = 1/\Sigma\, P_i^2$$

where P_i = proportion in category "i" (Levins 1968). Niche breadths were calculated for foraging height, foraging maneuver, and foraging substrate. Differences in niche breadths by habitat for each foraging variable were determined with a one-way analyses of variance (ANOVA) using JMP (SAS 1995). Niche overlaps were calculated using the formula:

$$O_{jk} = \Sigma\, P_{ia}P_{ja} \,/\, \sqrt{(\Sigma\, P_{ia}^2)\,(\Sigma\, P_{ja}^2)}\ .$$

where P_{ia} & P_{ja} = proportional use of resource state "a" by species "i" and "j" (Pianka 1974). Overlap values were calculated for the same foraging variables analyzed for the niche breadth calculations. A one-way analyses of variance (ANOVA) was then used to test for differences in overlap values between species grouped by forest type for each foraging variable using JMP; a Welch analysis of variance was calculated when variances were unequal (SAS 1995).

To assess the overall specialization of temperate and tropical bird species within each forest type, general variances were also calculated for each bird species in each habitat type. The general variance for each species was divided by the general variance for each respective forest type. This new value estimates the degree to which a species is specialized. It compares the variation available to a species in a forest type (the general variance of the random samples) to a species' use (the general variance for a species) in that same forest type. A species with a general variance equal to its respective forest would be an extreme generalist (Degree of generalization, hereafter DoG = 1.0), whereas a species with a general variance much lower than that of its respective forest would be a specialist (DoG near 0.0). A one-way analyses of variance was then performed between each group of species from each forest type using the derived DoG value using JMP (SAS 1995). When a bird species' mean was zero for a given variable, that variable had to be eliminated in the calculation of the general variance for that species within that habitat because zero values yielded singular matrices, from which it is impossible to calculate a general variance.

RESULTS

Habitat analyses.—For detailed quantification of habitat types by variable, see Marra (1989). Principal component analyses were unable to explain any significant amount of variance in the data. The first five factors explained only 42% of the variance with rotation and 37% without rotation. These results suggest that little multicolinearity exists among variables; therefore, none of the variables were combined or removed for other analyses. Furthermore, no other interpretations from these analyses were made due to dangers in interpreting factor analyses in which so little of the variance can be explained (Gibson et al. 1984).

To evaluate the complexity (= heterogeneity) of the understory within each forest type, the general variance was calculated from the variance-covariance matrix constructed from the random measurements. Among tropical forests, river-edge forest was highest at 79, then transitional forest at 65, and *terra firme* forest at 60 (Table 3). When data from tropical forests were combined, the general variance was 80. The temperate forest general variance fell between transitional and *terra firme* forest types with a value of 63 (Table 4). Therefore, assuming that the general variance is indeed a measure of habitat complexity, the understory of the combined tropical forests appear to be more complex structurally than the temperate forest. When analyzed separately, river-edge forest is the most complex, and the understories of transitional, temperate and *terra firme* forests are similar. Statistical tests between general variances are problematic, so values presented above for each habitat type are meant to be used as a relative index of overall habitat heterogeneity.

Macrohabitat selection.—At the temperate site, *Cardinalis cardinalis* and *Thryothorus ludovicianus* were the most common at 5.0 pairs per km, and *Wilsonia citrina* and *Oporornis formosus* were less common at 3.4 and 3.3 pairs respectively per km in bottomland hardwood forest (Table 5).

In tropical forest, six of the seven target species showed marked differences in abundance among forest types (Table 5). *Myrmoborus leucophrys* was more common in river-edge forest

TABLE 3

General Variance (Determinant) and "Degree of Generalization" (DoG) Values for Tropical Species within Each Forest Type and Forests Combined. DoG Values Are Calculated by Dividing the Determinant of a Given Species into That Forest Type. DoG Values Near 1.00 Would Be a Generalist, Whereas Those Near 0.0 a Specialist. Random Values Are the General Variances for a Given Forest Type. * One or More Values Were Eliminated in the Calculation of the General Variance (see text)

	River-edge		Transitional		Terra Firme		Combined	
	Determinant	DoG	Determinant	DoG	Determinant	DoG	Determinant	DoG
Mb. myotherinus	—	—	—	—	46	0.77	50	0.63
Mb. leucophrys	56	0.71	63	0.97	—	—	74	0.93
F. analis	41	0.52	52	0.80	—	—	69	0.86
F. colma	—	—	*38	0.58	*48	0.80	57	0.79
Mc. hemimelaena	*49	0.62	62	0.95	28	0.47	73	0.91
H. cantator	49	0.62	45	0.70	—	—	66	0.83
C. torquata	16	0.20	*27	0.42	*31	0.52	44	0.55
MEAN (± SE)		0.53 ± 0.08		0.73 ± 0.07		0.64 ± 0.09		0.78 ± 0.07
RANDOM	79		65		60		80	

than in transitional forest, and absent from *terra firme* forest. The congener *M. myotherinus* showed the opposite habitat preferences of *M. leucophrys*; it was common in *terra firme* forest, rare in transitional, and absent in river-edge forest. *Formicarius analis* was equally abundant in both river-edge and transitional forest, but rare in *terra firme* forest, where *F. colma* was common. The latter was uncommon in transitional forest, and rare in river-edge forest. *Myrmeciza hemimelaena* was common in all three forest types, although slightly more common in river-edge forest. *Hypocnemis cantator* was more common in river-edge forest than in transitional, and absent from *terra firme* forest. *Corythopis torquata* was present in all three forest types but most abundant in transitional forest.

Microhabitat selection.—For those variables in which selectivity was demonstrated, we plotted selectivity (use minus availability) for each category of microhabitat variable. Only six of these graphs will be presented for each species in each forest type; the remainder will be described and summarized in the text. A summary of these comparisons shows that temperate species significantly selected 45% (14/31) of the habitat variables. In contrast, selection was more frequent in the tropical forest birds. River-edge forest species selected 69% (24/35) of the microhabitat variables, transitional forest species 63% (22/35), and *terra firme* forest species 40% (14/35).

Temperate Forest Birds

In general, temperate species selected microhabitat with high densities of live and dead stems, and avoided areas with large amounts of airspace. Each species also exhibited a preference for some unique structural component (i.e., vines, suspended dead leaves, leaf litter) of bottomland

TABLE 4

General Variance (Determinant) and "Degree of Generalization" (DoG) Values for Temperate Forest Species. DoG Values near 1.00 Would Be Generalist, Whereas Those near 0.0, Specialist. RANDOM Value Is the General Variance for Temperate Forest

	Determinant	DoG
Cardinalis cardinalis	59	0.94
Thryothorus ludovicianus	71	1.13
Vireo griseus	70	1.11
Wilsonia citrina	57	0.90
Oporornis formosus	56	0.89
MEAN (± SE)		0.99 ± 0.08
RANDOM	63	

TABLE 5

RELATIVE ABUNDANCE OF TROPICAL AND TEMPERATE TARGET SPECIES WITHIN EACH FOREST TYPE (PAIRS/KM)

	Tropical species		
	River-edge	Transitional	Terra firme
Myrmoborus myotherinus	0.0	0.3	4.0
Mrymoborus leucophrys	5.0	2.3	0.0
Formicarius analis	3.0	3.3	1.0
Formicarius colma	0.5	2.3	3.0
Myrmeciza hemimelaena	5.0	4.0	3.5
Hypocnemis cantator	5.0	3.0	0.0
Corythopis torquata	1.0	3.7	1.5
TOTAL	19.5	18.9	13.0
	Temperate species		
Cardinalis cardinalis	5.0		
Thryothorus ludovicianus	5.0		
Vireo griseus	4.3		
Wilsonia citrina	3.4		
Oporornis formosus	3.3		
TOTAL	21.0		

hardwood forest. Therefore, at least when foraging, temperate species preferred areas with dense vegetation and did show signs of some specialization. Presumably, denser vegetation provides a higher density and diversity of prospective foraging substrates and greater concealment from predators.

Cardinalis cardinalis.—This species showed selectivity for 16% (5/31) of the microhabitat variables. It preferred 2-m cylinders with relatively low vine density (Fig. 1, $P \leq 0.025$) and avoided dense vine tangles. It also selected microhabitat containing palmetto in densities of 1—25% in 10-m cylinders, and it avoided areas where the volume of palmetto exceeded 25% in density ($P \leq 0.025$). A significant preference was also shown for 2-m cylinders with 0–40% air volume, and it avoided areas with more air space than this ($P \leq 0.001$).

Thryothorus ludovicianus.—This species selected 26% (8/31) of the microhabitat variables, more than any other target species in temperate forest (Fig. 2). It avoided microhabitat without any small stems (DBH 0–16 cm), preferring areas with at least 3–4 small stems in the 2-m cylinders ($P \leq 0.05$). It also avoided microhabitat that contained more than one stem in the DBH class of 32–50 cm (Fig. 2, $P \leq 0.025$) and strongly avoided those areas with stems >152 cm in the 10-m cylinders ($P \leq 0.01$). This species was the only temperate species to select microhabitat (2-m-cylinders) containing suspended dead leaves ($P \leq 0.001$) and avoided microhabitat without vines, preferring areas where the volume of vines was in the 11–50% range (Fig. 2, $P \leq 0.001$).

Vireo griseus.—This species selected 19% (6/31) of the microhabitat variables (Fig. 3). It avoided microhabitat with stems in the 32–50 cm DBH class ($P \leq 0.001$). It selected 2-($P \leq 0.001$) and 10-m ($P \leq 0.005$) cylinders where vine volume composed 11–75% of the cylinders. It also avoided microhabitat containing greater than 40% air space, preferring areas with denser vegetation ($P \leq 0.001$).

Wilsonia citrina.—This species selected 16% (5/31) of the habitat variables (Fig. 4). It preferred microhabitat with a taller canopy in the 15–22 m range and avoided microhabitat with a canopy lower than 15 m ($P \leq 0.001$). Within 2-m cylinders, areas with more than 40% air space were avoided and those with less air space were selected ($P \leq 0.001$). At the 10-m cylinder level of measurement, it avoided areas with small stems (DBH 0–16 cm) in densities of 30 or more ($P \leq 0.05$).

Oporornis formosus.—This species selected 19% (6/31) of the variables (Fig. 5). It preferred microhabitat with 3–6 leaves per point sample in the leaf litter and avoided areas with more than this both within 2- ($P \leq 0.01$) and 10-m cylinders ($P \leq 0.001$). It preferred 2-m cylinders with a volume of vines of 1–50% and avoided areas with no vines and where vine composition exceeded 50% ($P \leq 0.01$). Microhabitat (2-m cylinders) that exceeded 65% in open air space was avoided and areas less than this selected ($P \leq 0.001$).

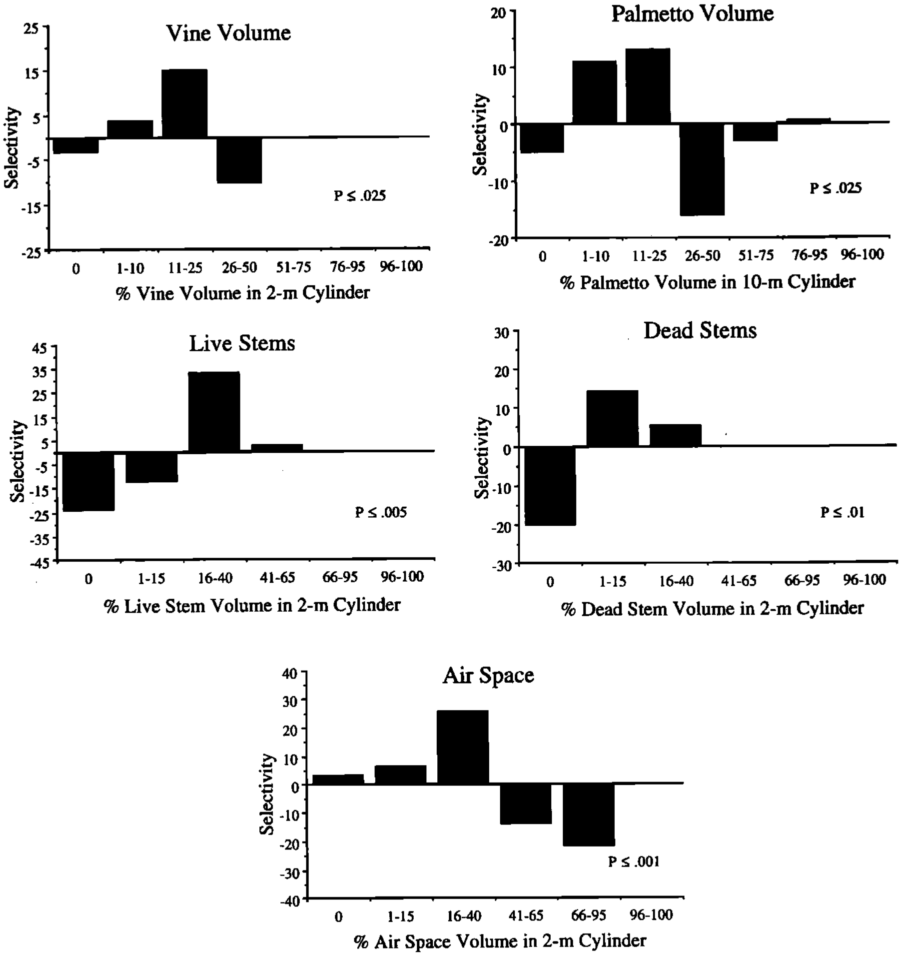


FIG. 1. Microhabitat selectivity in *Cardinalis cardinalis*. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

RIVER-EDGE FOREST BIRDS

Species of river-edge forest differed strongly in the microhabitat each selected. *Hypocnemis cantator* and *M. leucophrys* were similar in their selection of bamboo, although *H. cantator* showed a much greater preference. *Myrmeciza hemimelaena* generally preferred areas more typical of transitional forest than river-edge forest, whereas *C. torquata* selected microhabitat within river-edge forest more similar to *terra firme*.

Myrmoborus leucophrys.—This species selected 37% (13/35) of the habitat variables (Fig. 6). It avoided areas with dense (> 26%) ground cover, preferring areas with 11–25% cover ($P \leq 0.025$). Microhabitats with 50–95% shrub cover were preferred and areas with less than 50% avoided in 10-m cylinders ($P \leq 0.001$). Bamboo was selected at the 10-m cylinder level of measurement at densities greater than 15% ($P \leq 0.005$). Accordingly, microhabitat associated with bamboo was shown to be selected; 2-m cylinders were selected with three to four small stems and 10-m cylinders with densities of 61–100 small stems (0–16 cm DBH; $P \leq 0.005$). All larger DBH classes (from 32 cm) in 10-m cylinders, with densities greater than one, were avoided ($P \leq 0.001$). Dense leaf-litter was preferred (2- and 10-m; $P \leq 0.005$), whereas fallen logs (in 10-m cylinder; $P \leq 0.005$) and palms were avoided 10-m; $P \leq 0.001$).

Formicarius analis.—This species selected 11% (4/34) of the habitat variables (Fig. 7). It preferred 10-m cylinders with more than 40 small stems (DBH 0-16 cm; $P \leq 0.001$) and avoided areas with lower densities of stems in this size class (DBH 0-16 cm; $P \leq 0.001$). It avoided

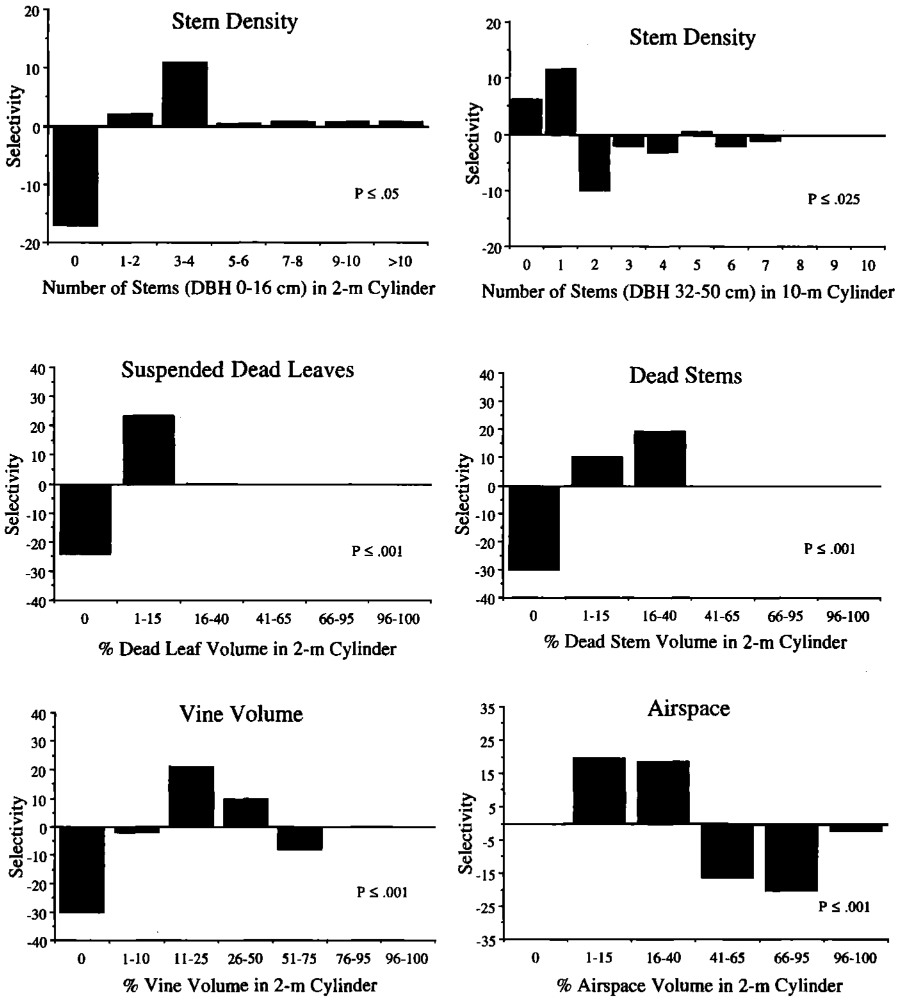


FIG. 2. Microhabitat selectivity in *Thryothorus ludovicianus*. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

10-m cylinders with larger stems (DBH 50–76 cm $P \leq 0.025$; DBH 76–152 cm $P \leq 0.005$) and with fallen logs ($P \leq 0.001$).

Myrmeciza hemimelaena.—This species selected 20% (7/34) of the habitat variables (Fig. 8). It avoided areas with canopy cover greater than 80% preferring areas with canopy cover between 30 and 70% ($P \leq 0.005$). Ground cover between 25–95% was preferred in the 2-m cylinders (Fig. 8, $P \leq 0.01$) and 26–75% in the 10-m cylinders ($P \leq 0.001$). This species avoided microhabitat in 2- and 10-m cylinders with bamboo ($P \leq 0.001$) or *Heliconia* ($P \leq 0.001$).

Hypocnemis cantator.—This species selected 37% (13/34) of the habitat variables (Fig. 9). The selection of bamboo was significant in both 2- and 10-m cylinders ($P \leq 0.001$). Similar to the habitat associations of *M. leucophrys*, variables positively correlated with bamboo were preferred (shrub cover, $P \leq 0.001$, and leaf litter [2-m cylinder, $P \leq 0.001$; 10-m cylinder, $P \leq 0.01$]) and variables not associated with bamboo avoided (stems 16–50 cm DBH in 10-m cylinder, $P \leq 0.001$; stems 50–76 cm DBH in 10-m cylinder, $P \leq 0.005$; stems 76–152 cm DBH in 10-m cylinder, $P \leq 0.025$; fallen logs in 10-m cylinder, $P \leq 0.001$, and palms in 2- [$P \leq 0.025$] and 10-m cylinders [$P \leq 0.005$]).

Corythopis torquata.—This species selected 29% (10/34) of the habitat variables (Fig. 10). It preferred areas where the canopy exceeded 22 m in height and avoided areas with a shorter

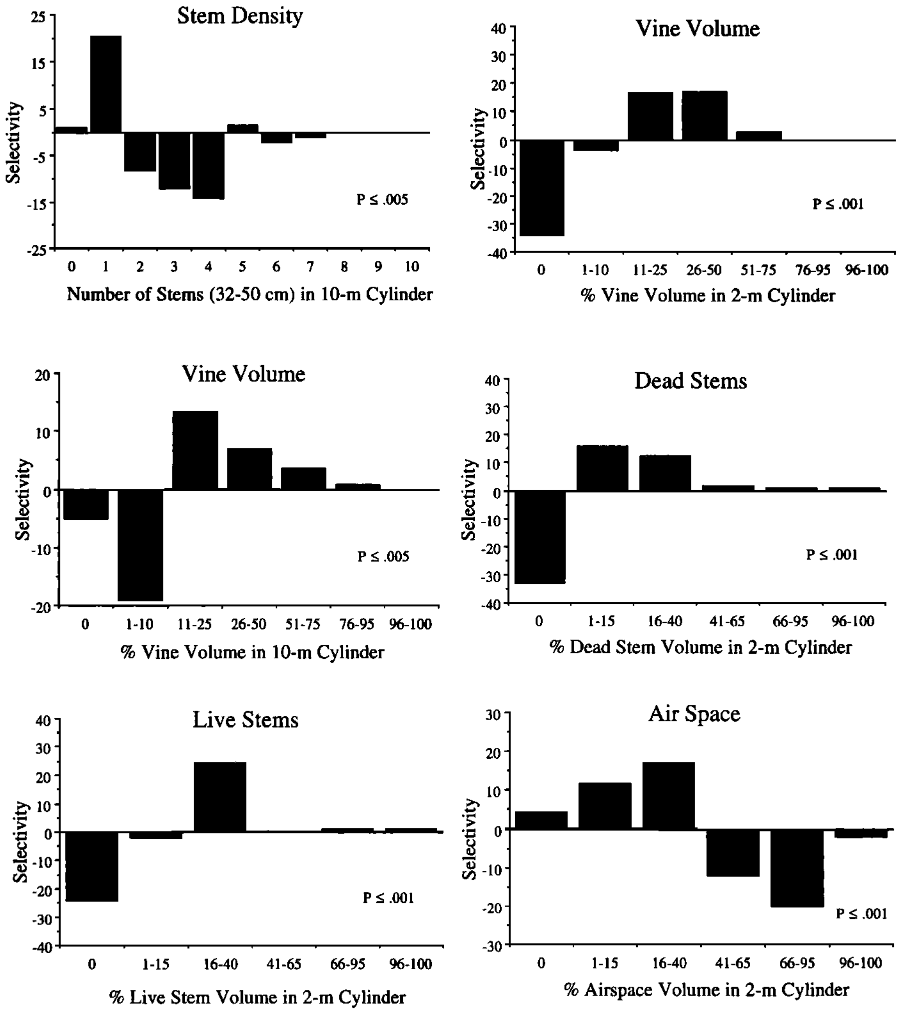


FIG. 3. Microhabitat selectivity in *Vireo griseus*. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

canopy ($P \leq 0.001$). Accordingly, areas with large stems (DBH > 152 cm; $P \leq 0.05$) were preferred, and it avoided microhabitat not associated with mature forest, such as small stems (DBH 0–16 cm; $P \leq 0.005$), shrub density greater than 25% (2-m cylinders, $P \leq 0.05$), and vine volume in excess of 10% (10-m cylinders, $P \leq 0.01$). This species preferred areas where the leaf litter was less than two leaves thick ($P \leq 0.001$). Areas containing bamboo were strongly avoided in both the 2- and 10-m cylinders ($P \leq 0.001$).

TRANSITIONAL FOREST BIRDS

In transitional forest, *H. cantator* and *M. leucophrys* showed even stronger selection for bamboo, which is much less extensive there than in river-edge forest. *Myrmeciza hemimelaena* and *C. torquata* were more generalized in microhabitat preference in transitional forest than in river-edge forest. This is probably because transitional forest is much more homogeneous compared to the structurally more heterogeneous river-edge forest (Table 3).

Myrmoborus leucophrys.—This species selected 29% (10/35) of the habitat variables (Fig 11). It showed a stronger selection for bamboo in transitional forest than it did in river-edge forest, both within 2-m and 10-m-cylinders ($P \leq 0.001$). Variables positively associated with bamboo were again also preferred by *M. leucophrys* (stems, DBH 0–16 cm in 2-m [$P \leq 0.01$], and 10-m

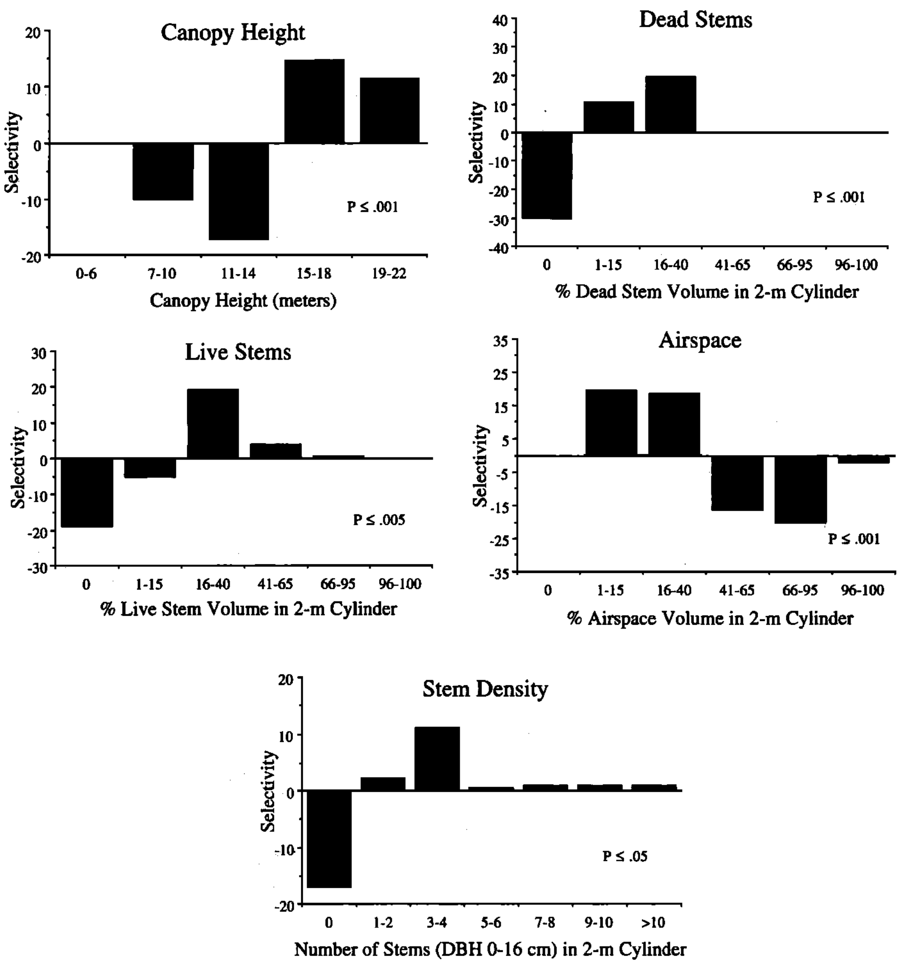


FIG. 4. Microhabitat selectivity in *Wilsonia citrina.* Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

cylinders [$P \leq 0.001$], dead stems [$P \leq 0.05$], and leaf litter [$P \leq 0.001$]), and it avoided variables negatively associated with bamboo (large stems, DBH > 50 cm, $P \leq 0.005$).

Formicarius analis.—This species selected 14% (5/35) of the habitat variables (Fig. 12). It preferred microhabitat with 70% canopy cover and avoided areas with less cover than this ($P \leq 0.001$). It preferred areas having a canopy of trees from 23 m to over 30 m ($P \leq 0.025$). Stems 32–50 cm in diameter were avoided when their densities were greater than 2 in 10-m cylinders ($P \leq 0.05$). Live stems in densities greater than 15% ($P \leq 0.01$) and shrub cover in densities greater than 25% ($P \leq 0.025$) were also avoided.

Formicarius colma.—This species selected 14 (5/35) of the habitat variables (Fig 13). It avoided areas containing trees with DBH's between 50–152 cm. This species avoided areas with bamboo ($P \leq 0.005$), whereas it preferred areas with *Heliconia* ($P \leq 0.05$). *Formicarius colma,* like *F. analis,* preferred areas with a canopy cover of 70–100% and avoided all areas with less than 70% ($P \leq 0.025$).

Myrmeciza hemimelaena.—This species showed little selectivity in this forest type. Only 9% (3/35) of the variables were selected (Fig 14). It preferred microhabitat with a canopy composed of trees of at least 23 m ($P \leq 0.005$). It also preferred 2-m ($P \leq 0.025$) and 10-m cylinders ($P \leq 0.01$) with high densities of stems in the 0–16 cm DBH class.

Hypocnemis cantator.—In contrast to *M. hemimelaena, H. cantator* was highly selective in transitional forest. It selected 43% (15/35) of the habitat variables (Fig. 15). There was again

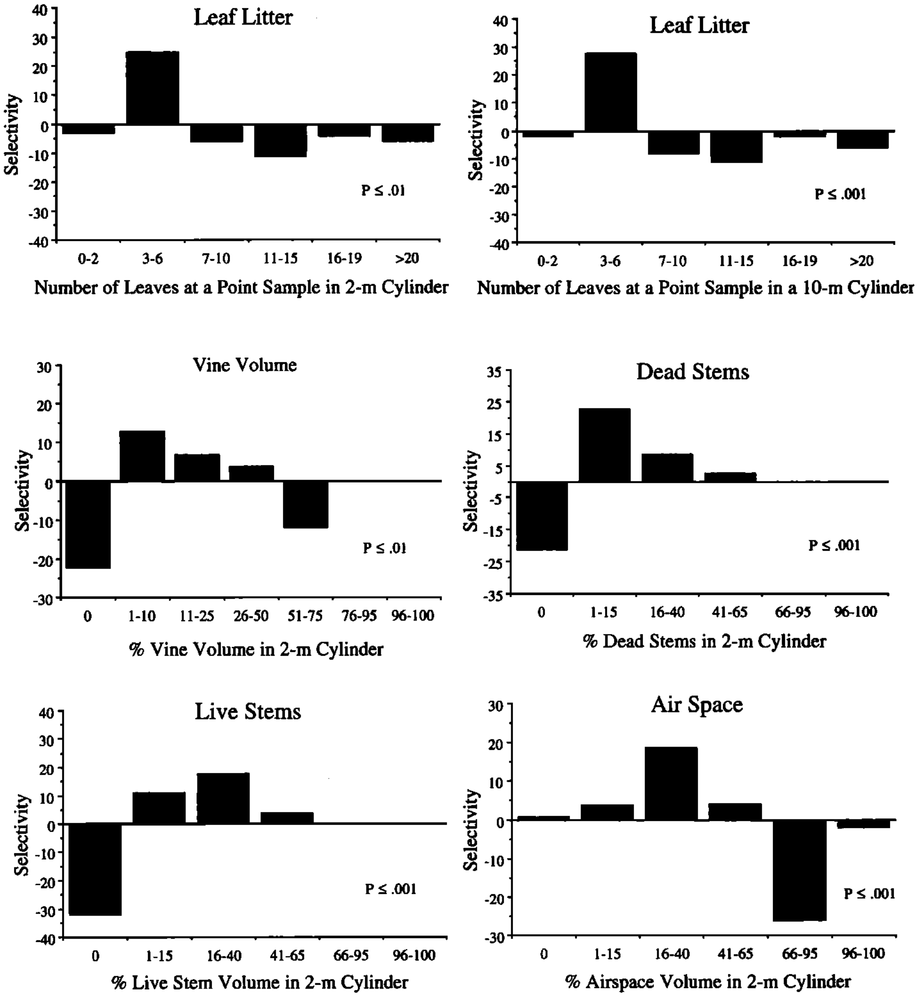


FIG. 5. Microhabitat selectivity in *Oporornis formosus*. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

strong statistical significance in its selection of microhabitat dominated by bamboo in 2-m ($P \leq 0.005$) and 10-m cylinders ($P \leq 0.001$). Accordingly, it preferred structural attributes associated with bamboo, such as small stems (DBH 0–16 cm: in 2-m cylinders, $P \leq 0.001$, and 10-m-cylinders, $P \leq 0.01$) and vines in 2-m cylinders ($P \leq 0.001$) and 10-m cylinders ($P \leq 0.01$), and it avoided variables not associated with bamboo, such as stems with DBH's between 16 and 152 cm ($P \leq 0.01$), fallen logs ($P \leq 0.01$), palms ($P \leq 0.01$), and airspace ($P \leq 0.01$). This species demonstrated preference for short trees (<10 m in height), avoided trees between 11 and 22 m, and preference for 23–30 m trees ($P \leq 0.001$). This preference corresponds to this species affinity for bamboo and treefall gaps.

Corythopis torquata.—This species selected 17% (6/35) of the habitat variables (Fig 16). It preferred areas with shrub cover between 1 and 25% and avoided areas with greater than 25% ($P \leq 0.005$). It avoided areas with a leaf litter of more than 2 leaves deep ($P \leq 0.01$), with vine volume more than 10% ($P \leq 0.001$), palms ($P \leq 0.025$), and bamboo ($P \leq 0.001$) in 10-m cylinders.

TERRA FIRME FOREST BIRDS

Species in *terra firme* forest tended to avoid areas with a tall canopy and preferred areas with more canopy cover. Areas with a thick leaf-litter were also avoided by all species.

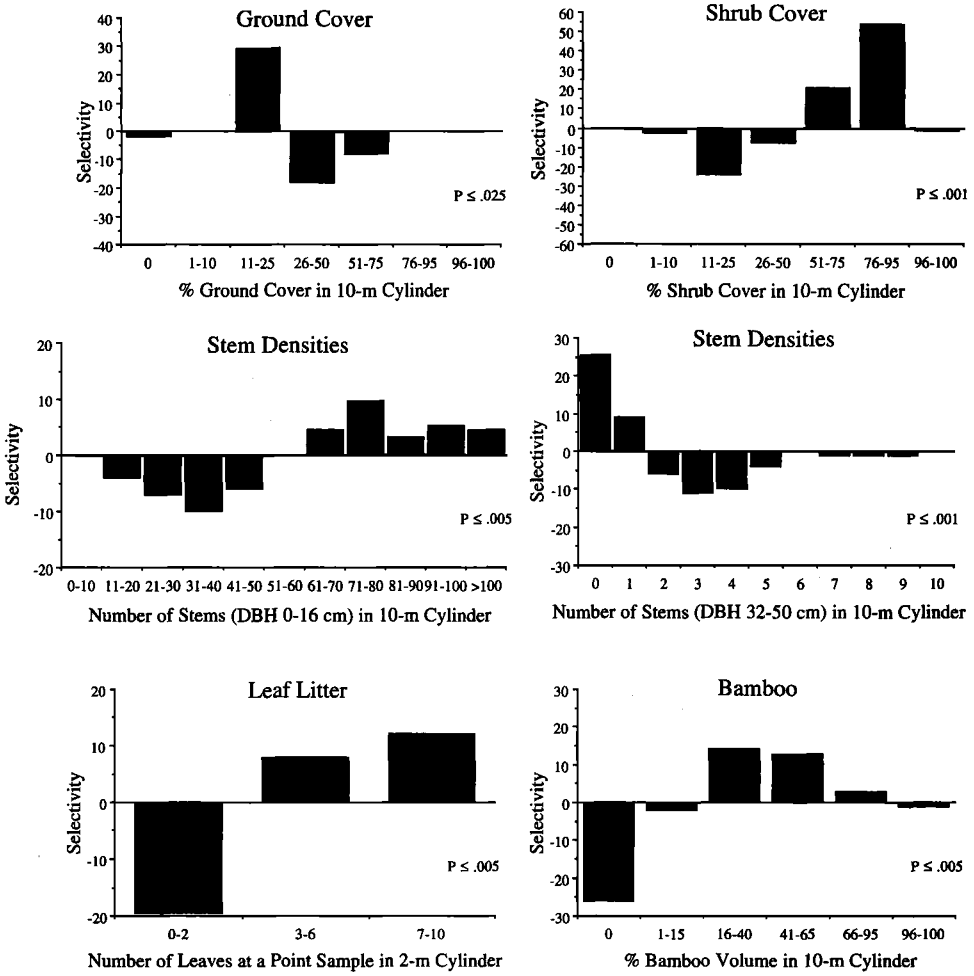


FIG. 6. Microhabitat selectivity in *Myrmoborus leucophrys* in river-edge forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

Myrmoborus myotherinus.—This species selected 23% (8/35) of the habitat variables (Fig. 17). It avoided areas where the canopy exceeded 27 m in height, preferring areas with a canopy 7–18 m ($P \leq 0.01$). Areas with canopy cover between 70 and 90% were also preferred ($P \leq 0.001$). This species avoided areas of shrub cover that exceeded 50%, preferring shrub cover in the 11-50% range ($P \leq 0.001$), and it preferred areas where the leaf litter was no more than 2 leaves thick ($P \leq 0.005$). This species also demonstrated preference for 2-m cylinders containing no suspended dead leaves ($P \leq 0.05$) and with live leaves in low densities (1–40%, $P \leq 0.001$), but it avoided areas with a densities of live leaves greater than 40%.

Formicarius colma.—This species selected 29% (8/35) of the habitat variables (Fig. 18). It preferred areas where the canopy was 7–22 m in height and avoided areas where the canopy height exceeded 22 m ($P \leq 0.001$). Shrub cover in 2-m cylinders greater than 25% was avoided ($P \leq 0.005$), and shrub cover in 10-m-cylinders greater than 50% was avoided ($P \leq 0.025$). It avoided areas containing stems ranging in DBH from 32 to 76 cm ($P \leq 0.005$). It preferred areas with leaf litter only 0–2 leaves thick in both 2-m and 10-m cylinders ($P \leq 0.001$). It also preferred sites containing less then 40% live leaf volume at the 2-m cylinder scale of measurement ($P \leq 0.001$).

Myrmeciza hemimelaena.—This species selected 20% (7/35) of the habitat variables (Fig. 19). In contrast to its selectivity in river-edge forest, it preferred areas where canopy cover was 80–

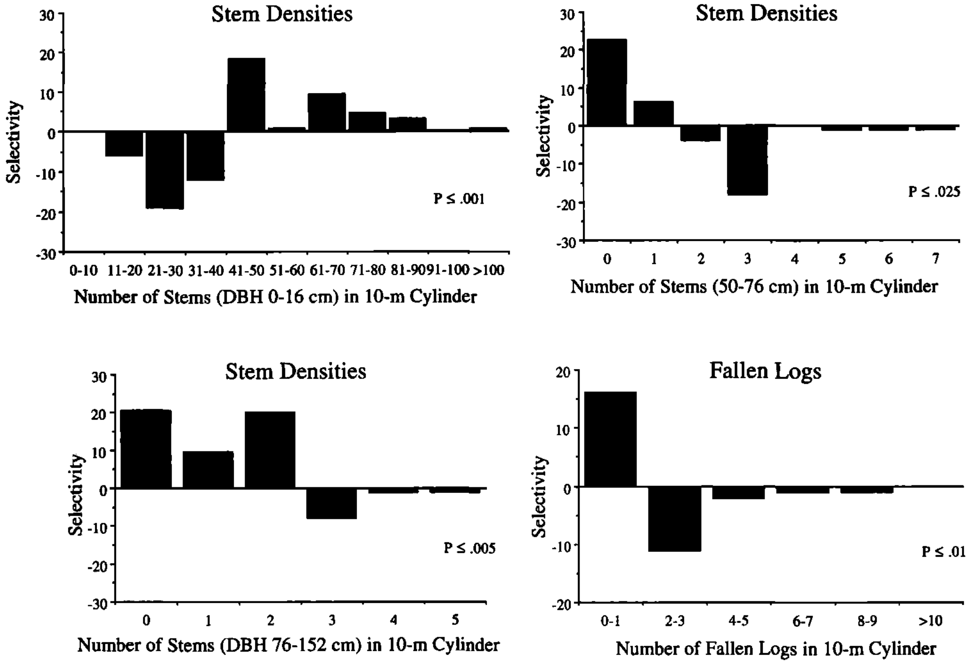


FIG. 7. Microhabitat selectivity in *Formicarius analis* in river-edge forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

90% ($P \leq 0.001$). This species preferred microhabitat having a density of 0–16 cm stems, ranging from 50 to 100 stems in 10-m cylinders ($P \leq 0.001$). Large stems with DBH's 32–76 cm were avoided in 10-m cylinders ($P \leq 0.001$). Areas with leaf litter 0–2 leaves in depth were preferred, and those areas where leaf litter exceeded this were avoided ($P \leq 0.001$). Palms were also avoided at the 10-m cylinder scale of measurement ($P \leq 0.001$).

Corythopis torquata.—This species selected 29% (10/35) of the habitat variables (Fig 20). In contrast to its preference in river-edge forest, *C. torquata* preferred forest with a shorter canopy, ranging between 15 and 22 m and with a canopy cover between 70 and 90% ($P \leq 0.001$). This species consistently foraged in areas with 11–25% ground cover, and avoided places with denser ground cover ($P \leq 0.005$). It avoided areas with shrubs exceeding 25% in 2-m cylinders and avoided areas exceeding 50% shrub cover in 10-m cylinders ($P \leq 0.001$). Like the other species in this habitat, it preferred thin leaf-litter (0–2 leaves) and avoided areas with a deep leaf litter ($P \leq 0.01$). Other sites avoided were those that included dense vines (>10%, $P \leq 0.025$), suspended dead leaves ($P \leq 0.001$), and dense live leaves (>40%; $P \leq 0.001$).

FORAGING BEHAVIOR

TEMPERATE BIRD SPECIES

Foraging maneuver and substrate.—The primary foraging maneuver used by *C. cardinalis* was gleaning (Fig. 21). Sally-strikes were the next most frequent maneuver, followed by flaking. *Cardinalis cardinalis* searched primarily live leaves and secondarily palmetto (Fig. 22). This corresponds to the results showing its preference for microhabitat containing palmetto (Fig. 1). All ten substrates used as foraging substrates by other temperate species were used by *C. cardinalis*.

Thryothorus ludovicianus gleaned substrates for prey almost as much as it probed them (Fig. 21). It flaked leaves in the leaf litter as well, but at a lower frequency. *Thryothorus ludovicianus* foraged on eight of ten substrates used by all species (Fig. 22) with almost equal frequency in each substrate. Dead leaves were the most frequently searched substrate, but only slightly more frequently than live leaves. Remsen and Parker (1984) and Rosenberg (1990) reported dead leaves as the predominant foraging substrate for tropical members of the genus *Thryothorus*, but

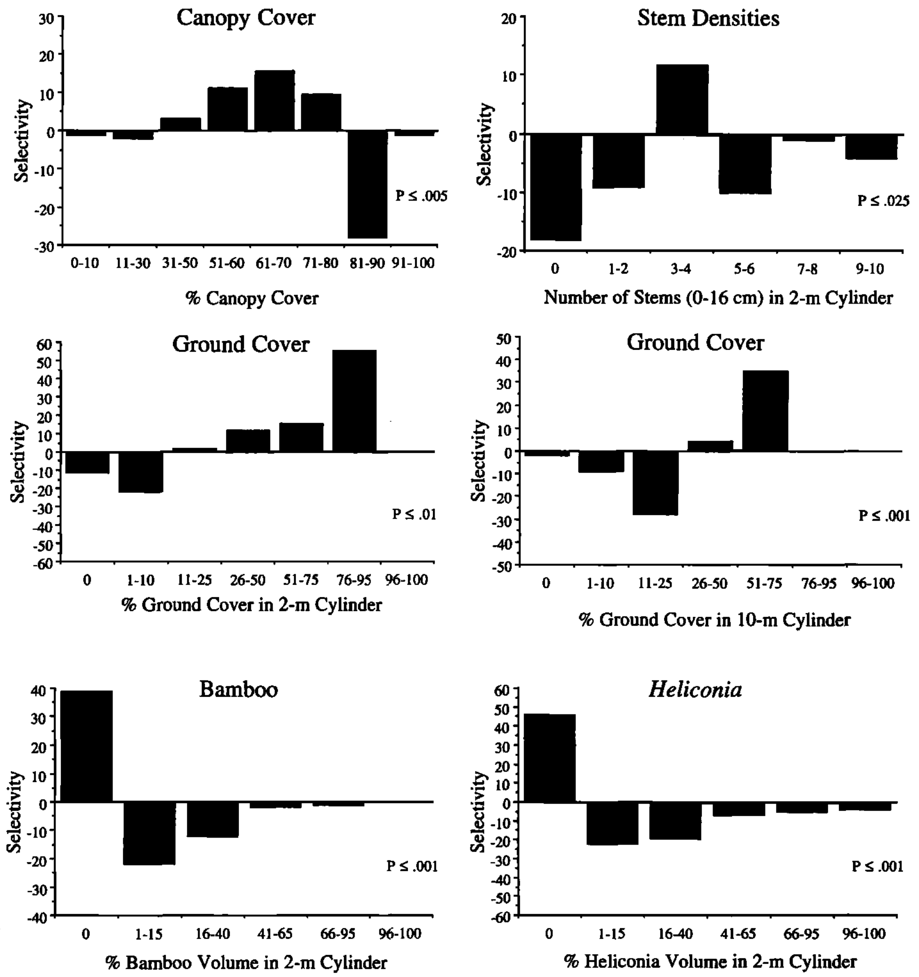


FIG. 8. Microhabitat selectivity in *Myrmeciza hemimelaena* in river-edge forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

these are the first data to document this for *T. ludovicianus*. This is also in accordance with our results from microhabitat use that found *T. ludovicianus* to prefer 2-m cylinders containing suspended dead leaves (Fig. 2).

Vireo griseus used only a narrow range of foraging maneuvers (Fig. 21). It used predominantly sally-strikes followed by gleans. Thus its foraging maneuvers are similar to those of three other vireos of eastern North America, *V. solitarius*, *V. olivaceus*, and *V. philadelphicus*, studied by Robinson and Holmes (1982). *Vireo griseus* foraged primarily on live leaves and secondarily on vines (Fig. 22). Microhabitat (2-m and 10-m cylinders) with high vine volume was preferred by *V. griseus* (Fig. 3).

Wilsonia citrina used predominantly gleans and sally-strikes (Fig. 21). It occasionally used sally-hovers and was the only species that used flutter-chases. Foraging by *W. citrina* was directed primarily towards live leaves and much less frequently at vines, dead stems, air, live stems, bark, and dead leaves (Fig. 22).

Oporornis formosus, like other temperate species, used predominantly gleans (Fig. 21). Sally-striking, flaking, and leaping were also observed at lower frequencies. *Oporornis formosus* was somewhat generalized in substrate use (Fig. 22). All ten substrates used by the other temperate species were also used by *O. formosus*. Although most foraging maneuvers were directed toward

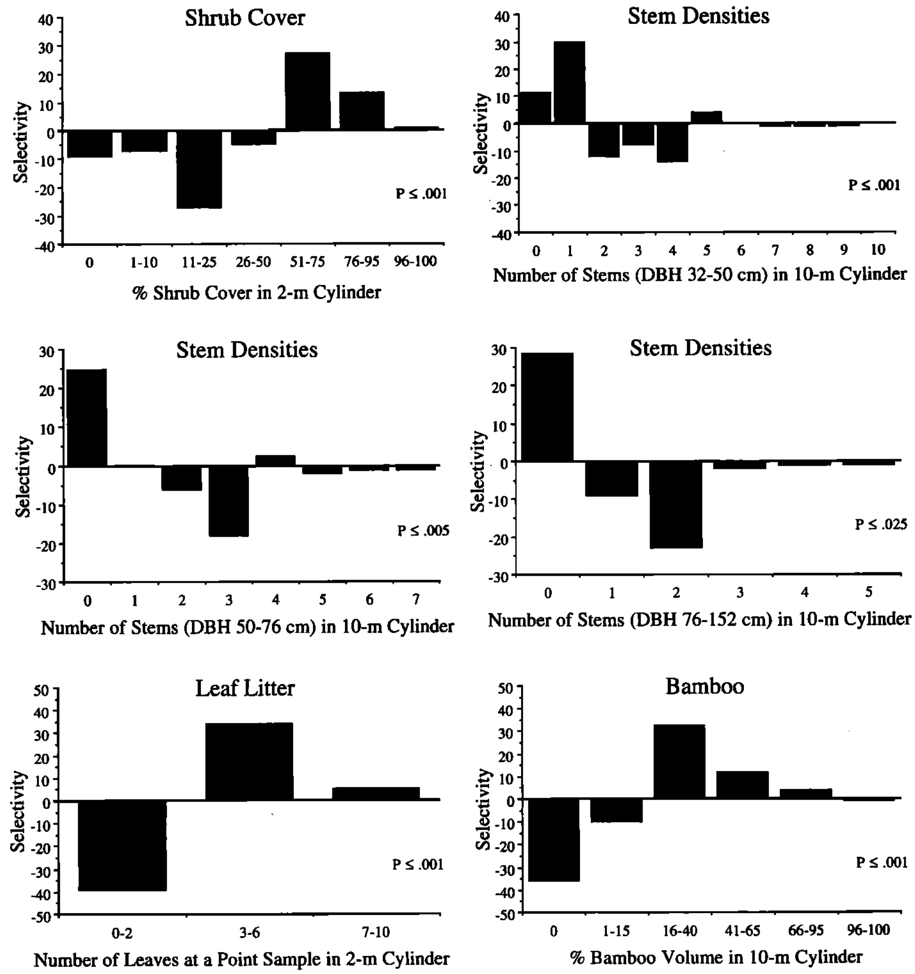


FIG. 9. Microhabitat selectivity in *Hypocnemis cantator* in river-edge forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

live leaves, it used vines, palmettos, live stems, and dead stems each in more than 10% of the observations.

Foraging height.—*Cardinalis cardinalis* foraged from the ground to the canopy (mean foraging height 3.3 m ± 3.2; Fig. 23). *Thryothorus ludovicianus* foraged from the ground to the midstory (mean foraging height 1.7 m ± 1.8; Fig. 23). *Vireo griseus* was also highly variable in its foraging height (mean foraging height 4.6 m ± 2.9; Fig. 23). It most often foraged by working its way up vine tangles into the canopy. The mean foraging height for *W. citrina* was the same as that for *V. griseus* (4.6 m ± 2.9; Fig. 23); *Wilsonia citrina* foraged from the ground to the subcanopy. *Oporornis formosus* foraged lower and was less variable than other temperate forest species (mean foraging height of 1.5 m ± 1.5; Fig. 23); much of its foraging was on the ground or in understory saplings.

TROPICAL FOREST SPECIES

Foraging maneuver.—Gleaning was the most frequently used maneuver by *H. cantator* (Fig. 24). It used all maneuver types with essentially the same frequency in river-edge and transitional forests except for hanging, which it used only in river-edge forest. Gleaning was the maneuver

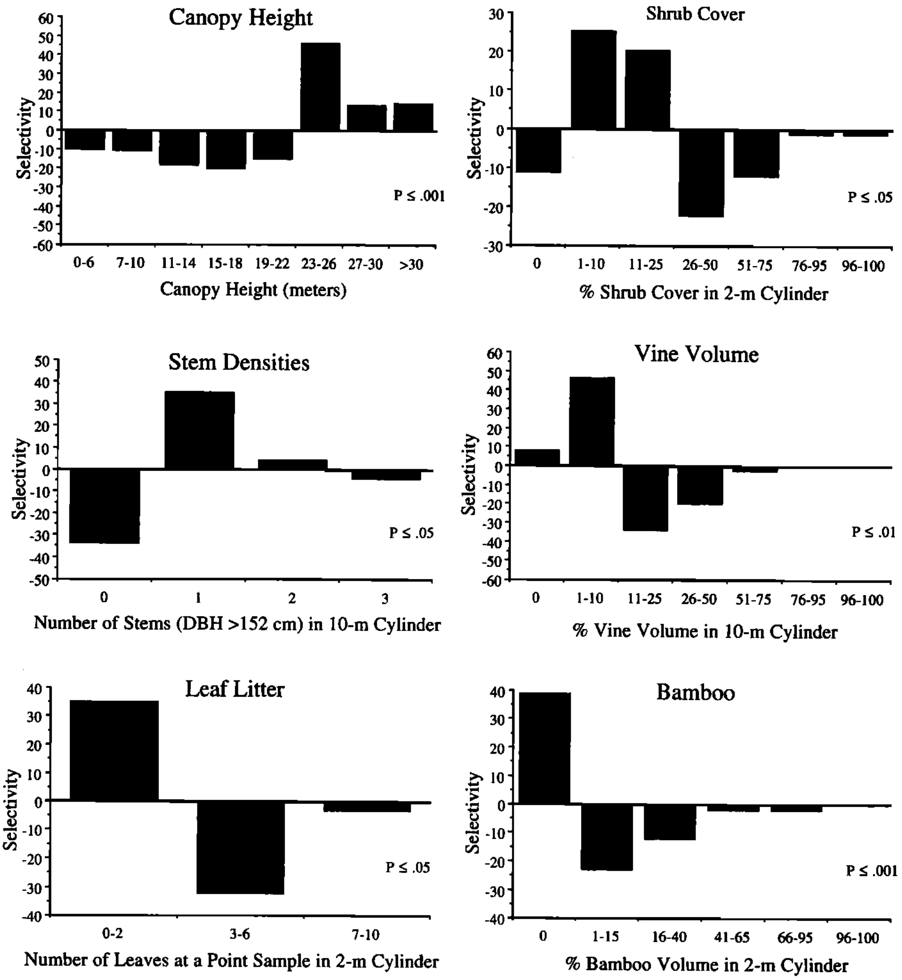


FIG. 10. Microhabitat selectivity in *Corythopis torquata* in river-edge forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

used most frequently by *M. hemimelaena* (Fig. 24), with leaping (from the forest floor up to foliage) used slightly less frequently. In general, it used all maneuvers with the same frequency in each forest type. The primary foraging maneuver of *M. leucophrys* also was gleaning, with nearly the same frequency in both river-edge and transitional forests (Fig. 24). It used sally-strikes substantially more in river-edge than in transitional forest. The primary foraging maneuvers of *M. myotherinus* were gleaning and flaking (Fig. 24). It also used leaping, sally-striking, and flutter-chasing. Gleaning and flaking were the primary maneuvers used by *F. analis* in river-edge forest (Fig. 24). In transitional forest, however, it used gleaning about twice as frequently as flaking. Gleaning was the primary foraging maneuver used by *F. colma,* and flaking secondarily, in both transitional and *terra firme* forests (Fig. 24). Most foraging maneuvers used by *C. torquata* were either gleans, leaps, or flutter-chases (Fig. 24), as found by Fitzpatrick (1980). Most were used with the same frequency in all three forest types. Leaps were typically launched from the forest floor up to ground cover and even to low shrubs. Flutter-chasing was used less frequently in *terra firme* forest, where gleaning was used more often.

Foraging substrate.—Live leaves and bamboo leaves were the most frequently used substrates by *H. cantator* in both forest types; suspended dead leaves were used much more frequently in river-edge forest (Fig. 25). *Myrmeciza hemimelaena* used seven types of substrates in both river-

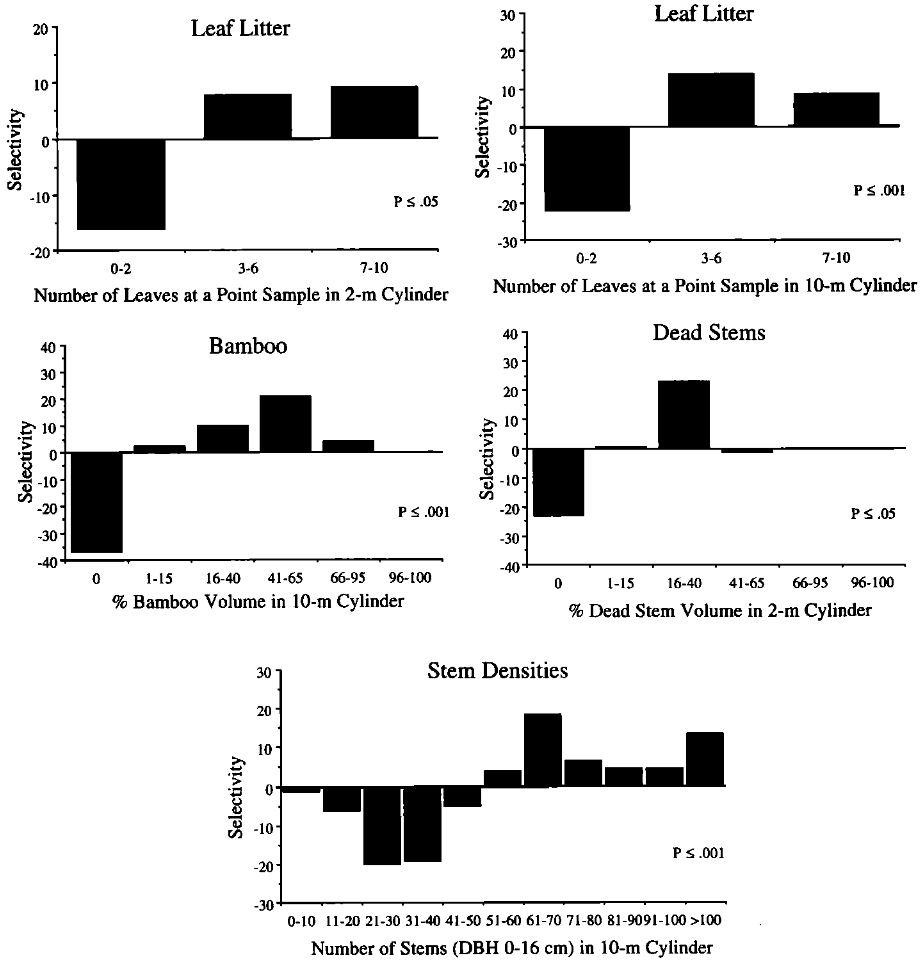


FIG. 11. Microhabitat selectivity in *Myrmoborus leucophrys* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

edge and transitional forest, but only four in *terra firme* forest (Fig. 25). *Myrmeciza hemimelaena* used most of the foraging substrates, each with less than 15% of the observations, and with roughly the same frequency in all forest types. *Myrmoborus leucophrys* used ten substrate types in river-edge forest and seven in transitional forest (Fig. 25). Live leaves and leaf litter were the predominant foraging substrates in river-edge forest, and live leaves, dead stems, leaf litter, and bamboo stems were used most frequently in transitional forest. *Myrmoborus myotherinus* foraged primarily in the leaf litter and on live leaves (Fig. 25). Nearly 100% of the foraging observations of *F. analis* in both forest types were in leaf litter (Fig. 25). *Formicarius colma* used predominantly leaf litter in both forest types (Fig. 25). *Corythopis torquata* most frequently used live leaves, leaf litter, and air in all three forest types (Fig. 25). Air was used substantially less frequently in *terra firme* forest than in any other forest type.

Foraging height.—*Myrmoborus myotherinus* foraged primarily on the ground, with a mean foraging height of 0.3 m (Fig. 23). The mean foraging height of *M. leucophrys* was 0.8 m ± 0.8 in river-edge forest but almost twice as high in transitional forest, with a mean of 1.4 m ± 1.5 (Fig. 23). *Formicarius analis* and *F. colma* were exclusively ground-foragers (mean height 0.0; Fig. 23). *Myrmeciza hemimelaena* had nearly the same mean foraging heights in river-edge (0.6 m) and transitional forests (0.5 m). In *terra firme* forest, however, it foraged much higher

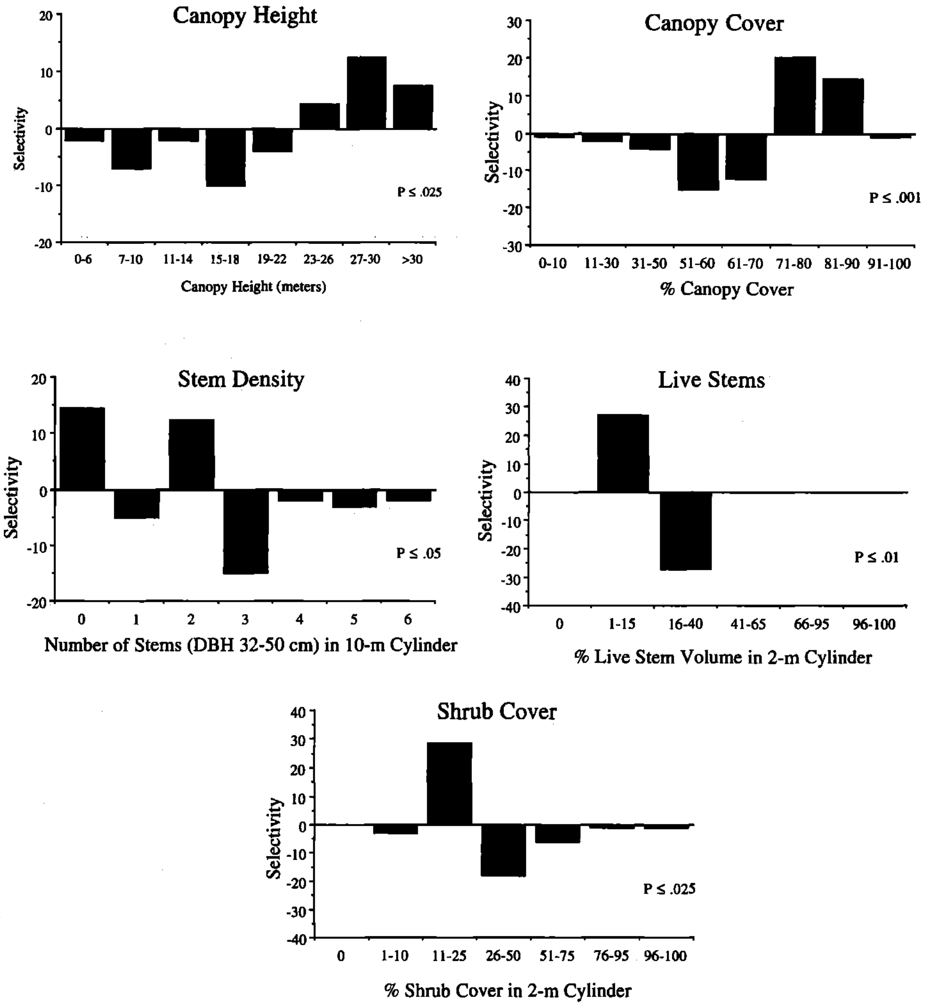


FIG. 12. Microhabitat selectivity in *Formicarius analis* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

(mean 1.2 m ± 1.2; Fig. 23). *Hypocnemis cantator* had mean foraging heights of 3.5 m ± 1.4 in river-edge forest and 4.1 m ± 1.6 in transitional forest (Fig. 23). There was high variation associated with each of these. This species was most commonly found in bamboo patches (Figs. 9, 15), where it had an especially broad vertical foraging range. *Corythopis torquata* had mean foraging heights of 0.02 m ± 0.05 in river-edge and 0.02 m ± 0.04 in transitional forests, and 0.01 m in *terra firme* forest (Fig. 23). Although this species is almost exclusively a ground-dwelling flycatcher, it occasionally forages from low perches to above-ground foliage.

TEMPERATE-TROPICAL COMPARISONS

NICHE BREADTHS

Comparisons of mean niche breadths for species of temperate and tropical forests for each foraging category (Fig. 26) reveal both similarities and differences. For all species-specific niche breadths, see Marra (1989). No differences were found between habitats in foraging maneuver breadth (ANOVA $F_{3,16} = 0.95$, $P = 0.44$). Therefore, these temperate and tropical species use a similar range of maneuvers in each of their respective forest types. No differences were found between habitats in breadth of substrates either (ANOVA $F_{3,16} = 1.3$, $P = 0.31$). However,

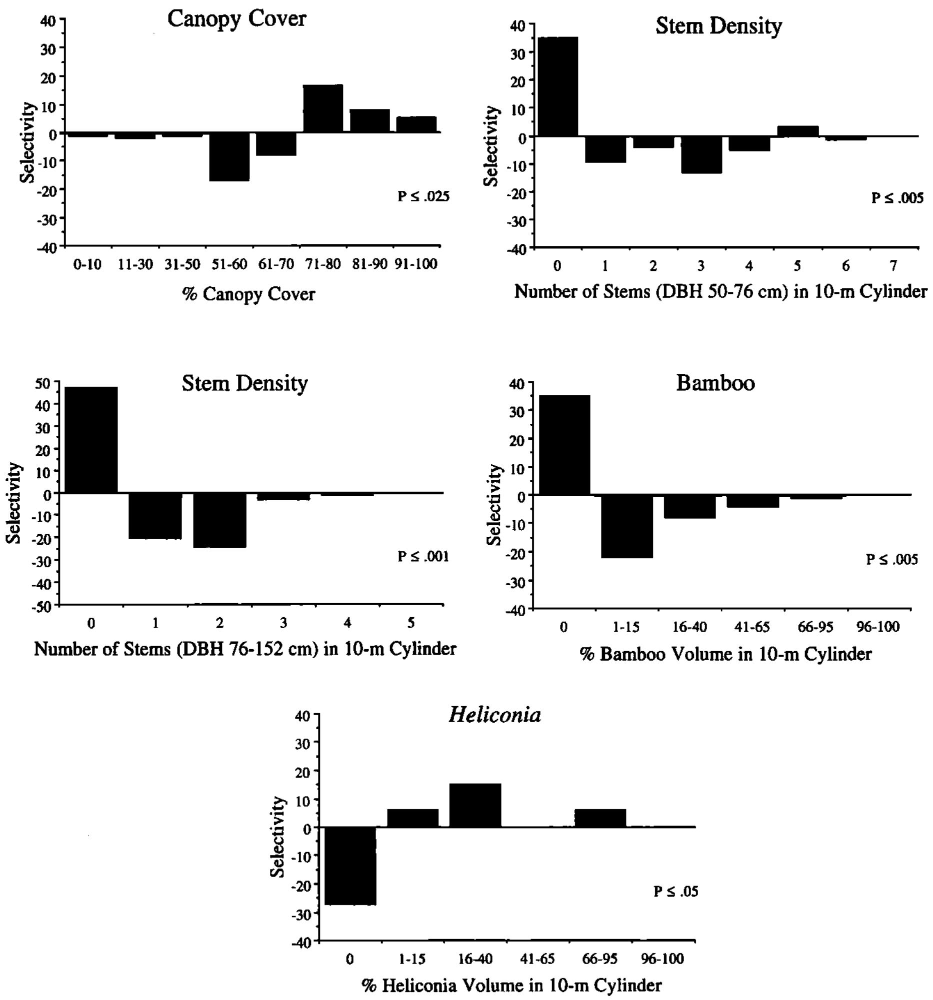


FIG. 13. Microhabitat selectivity in *Formicarius colma* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

temperate forest species did tend to use a broader range of substrates: their mean (3.8 ± 0.8) was higher than those of any of the tropical forest species (river-edge 2.8 ± 0.5, transitional 2.8 ± 0.5, *terra firme* 2.1 ± 0.3), suggesting greater substrate specialization by the tropical species (Fig 26).

With regards to foraging height, temperate forest birds had a significantly broader mean breadth (10.7 ± 1.1; ANOVA $F_{3,16} = 9.5$, $P = 0.0008$) than birds of any of the tropical forest types (Fig 24). *Terra firme* forest species had the lowest mean breadth in foraging height (2.7 ± 1.1), followed by river-edge (3.4 ± 1.3), and then transitional forest (3.6 ± 1.2) species. Certain tropical species had comparatively high foraging height breadths. Two bamboo specialists, *Myrmoborus leucophrys* and *Hypocnemis cantator*, species specializing horizontally (in this case on bamboo) are not comparably specialized vertically. This can also be seen with *Myrmeciza hemimelaena*, a species strongly associated with treefall gaps (another form of horizontal specialization; Marra 1989). Its foraging-height breadths were slightly higher than species not specializing on a horizontal component of the forest. This is especially clear in *terra firme* forest, where its foraging height breadth was broader, and its association with treefall gaps stronger, than in any other forest type (Marra 1989).

To summarize results on niche breadths, temperate understory species used a broader range of the vertical dimension of the habitat, relative to tropical understory species. Only tropical

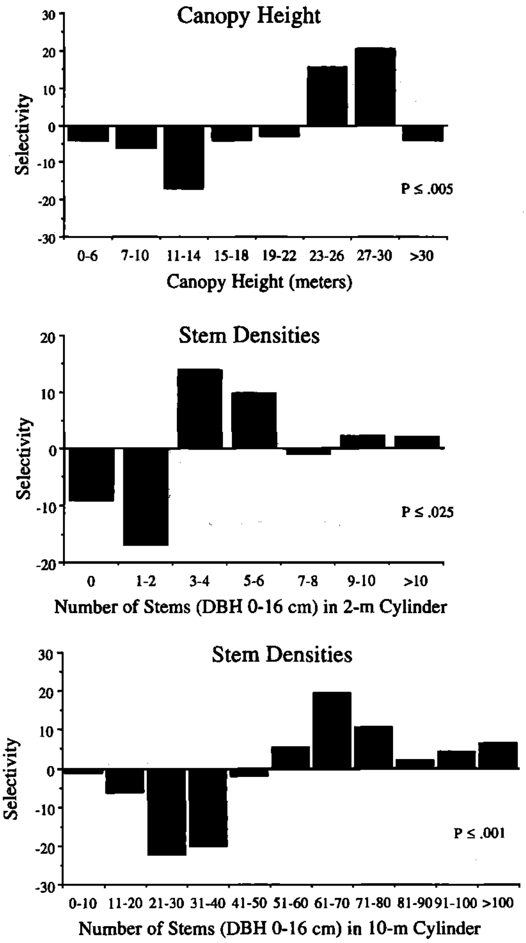


FIG. 14. Microhabitat selectivity in *Myrmeciza hemimelaena* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

species specializing "horizontally" have foraging height breadths as broad as those of temperate species.

NICHE OVERLAPS

Comparing overlap values from different forest types is fraught with interpretational problems. Nevertheless, we provide some cautious interpretations. The degree to which species overlap within each forest type with respect to foraging maneuver was marginally significant (ANOVA $F_{3,37} = 2.6$, $P = 0.06$; Fig 27). River-edge species showed less overlap in all types of foraging maneuvers used (0.65 ± 0.05) compared to species of temperate (0.79 ± 0.05), transitional (0.82 ± 0.03), and *terra firme* (0.85 ± 0.05) forests.

Temperate forest species (0.83 ± 0.05) showed significantly more overlap than tropical species (river-edge 0.61 ± 0.09, transitional 0.55 ± 0.09, *terra firme* 0.71 ± 0.10) in their use of foraging substrates (Welch ANOVA $F_{3,37} = 3.4$, $P = 0.04$; Fig 27). This result combined with those on niche breadth (Fig. 26) suggest greater substrate specialization by tropical forest species.

With respect to overlap in foraging height, species of temperate (0.66 ± 0.05) and *terra firme* (0.75 ± 0.09) forest overlapped slightly more in foraging height than did species of river-edge (0.43 ± 0.12) and transitional (0.47 ± 0.10) forest (Welch ANOVA $F_{3,37} = 2.4$, $P = 0.10$; Fig 27).

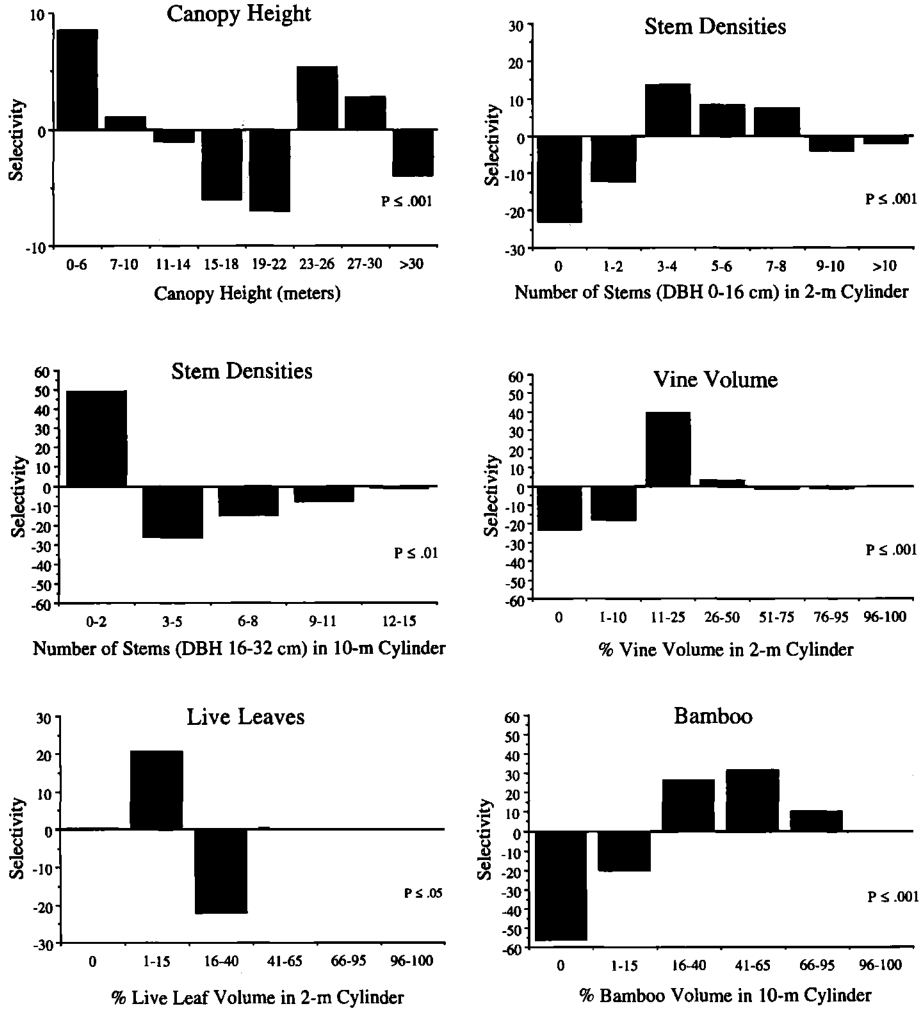


FIG. 15. Microhabitat selectivity in *Hypocnemis cantator* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

MULTIVARIATE ANALYSIS

All temperate species had general variances exceeding 0.89, and two species had values greater than 1 (Table 4). The latter result was due to these species having higher variances for some variables than recorded in the random samples. In river-edge and transitional forests, *C. torquata* and *M. leucophrys* had the lowest and highest DoG values respectively (ranging from 0.20 to 0.97; Table 3). Species in *terra firme* forest had DoG values ranging from 0.47 in *M. hemimelaena* to 0.80 in *F. colma* (Table 3). All DoG values for tropical forest species were significantly lower than those of temperate forest birds (ANOVA $F_{3,16} = 5.8$, $P = 0.007$). Therefore, these understory bird species of tropical forests are more specialized in their habitat selection than the temperate forest species.

A final illustration of the overall degree of specialization by both the temperate and tropical species can be demonstrated by plotting the DoG, an estimate of horizontal use of space, against both (1) the breadth of the foraging site (Σ of foraging maneuver breadth and foraging substrate breadth for each species; Fig. 28) and (2) breadth of foraging height, which is an estimate of vertical use of space (Fig. 28). The first figure illustrates how temperate and tropical species overlap heavily in those niche dimensions related to the breadth of their foraging sites (i.e.,

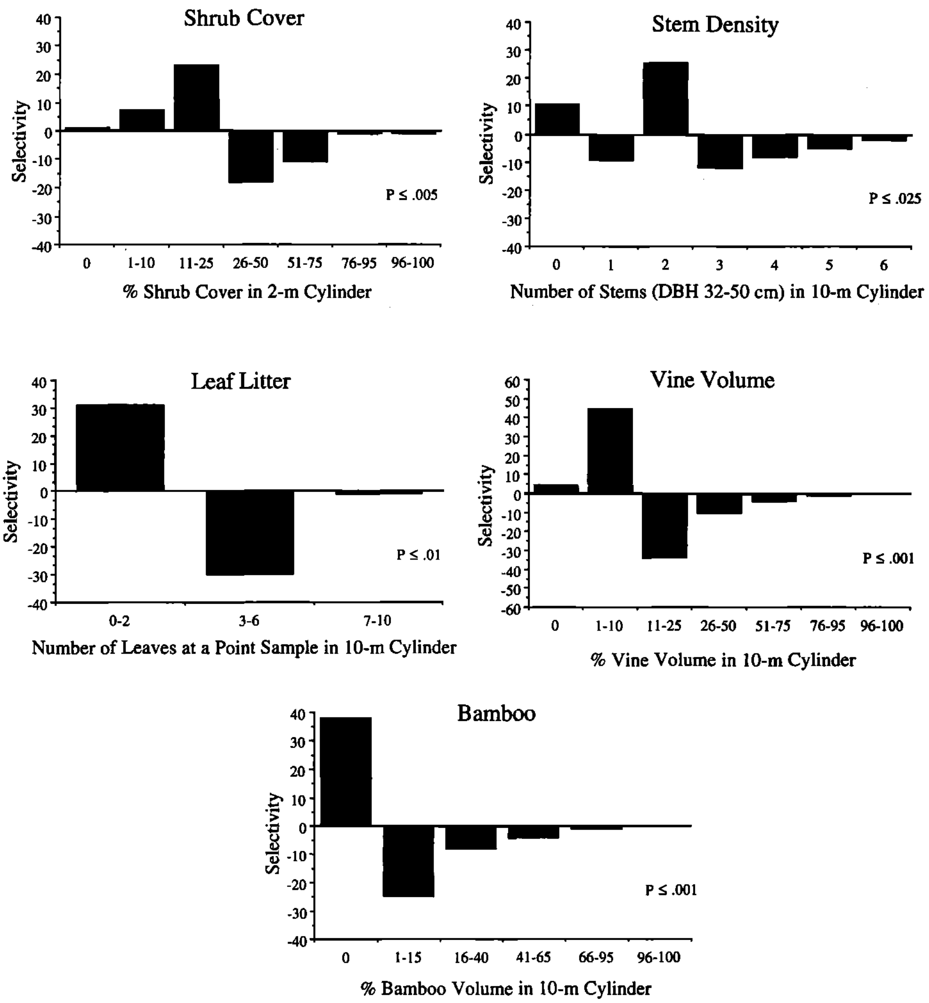


FIG. 16. Microhabitat selectivity in *Corythopis torquata* in transitional forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

maneuvers and substrates), whereas the two groups still differ strongly in degree of horizontal generalization, with temperate species significantly more generalized than tropical. This second comparison (Fig. 28) demonstrates the high degree of specialization by understory tropical species relative to temperate species in both a vertical (i.e., breadth of foraging height) and horizontal (i.e., degree of generalization) use of space.

DISCUSSION

Our goal was to investigate the proximate, ecological factors rather than the ultimate, evolutionary causes of high tropical species diversity. To do this, comparisons to less diverse areas such as temperate zone forests are necessary. Tropical-temperate comparisons have been conducted between birds of alder forests (Stiles 1978), woodpeckers (Askins 1983), wading birds (Kushlan et al. 1985), and understory birds in general (Karr 1971). That there are a myriad of complications inherent in any intercommunity comparison such as these is well known (Terborgh and Robinson 1986). However, we see no alternative to these comparisons for increasing our understanding of tropical diversity.

Are tropical habitats structurally more complex?—Few quantitative analyses have attempted to measure the complexity of tropical habitats. Until now, either foliage-height-diversity profiles

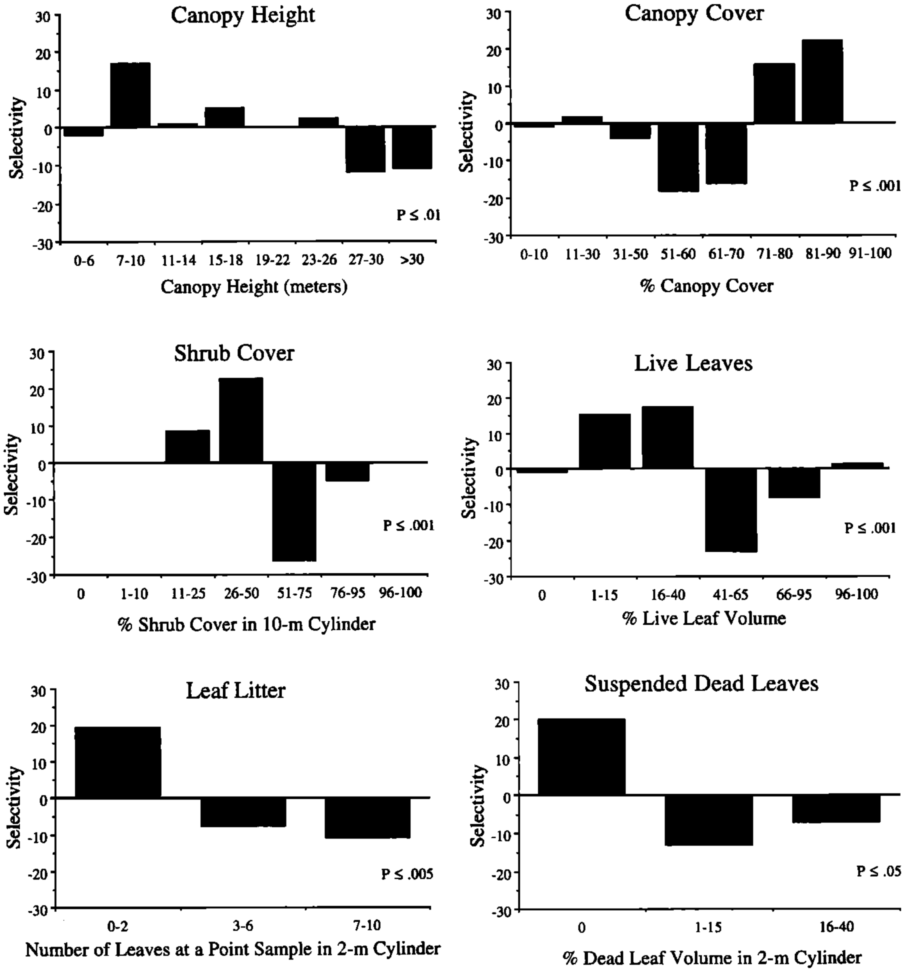


FIG. 17. Microhabitat selectivity in *Myrmoborus myotherinus* in *terra firme* forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

have been used to gauge the complexity by looking at forest stratification (MacArthur et al. 1966; Smith 1973), or tropical habitats have simply been accepted as more complex based upon qualitative descriptions. A foliage-height-diversity profile is an index of the vertical foliage density from the ground to the canopy. Studies using these indices have shown only a correlation between increasing vertical foliage density and higher species diversity (MacArthur and MacArthur 1961; MacArthur et al. 1962; MacArthur et al. 1966; Karr 1971; Karr and Roth 1971); others have found no such correlation (Orians 1969; Terborgh and Weske 1969; Howell 1971; Pearson 1975). Moreover, the effect that this type of complexity has on bird species restricted to the understory is unknown.

Before understanding the effects that increased habitat complexity might have on bird species diversity, it is necessary to define what is meant by habitat complexity. Habitat complexity can be examined at two different scales: (1) between habitats, i.e., more distinct kinds of habitats available, and (2) within-habitats, i.e., either more different layers of vegetation, or unique structural features, such as bamboo, palms, suspended dead leaves, epiphytes, or lianas. We focused on within-habitat complexity, whether tropical habitats are structurally more complex, and whether bird species diversity is related to this complexity.

We analyzed the structural complexity of just the understory of each forest type separately (temperate and tropical). Many variables differed significantly between temperate and tropical

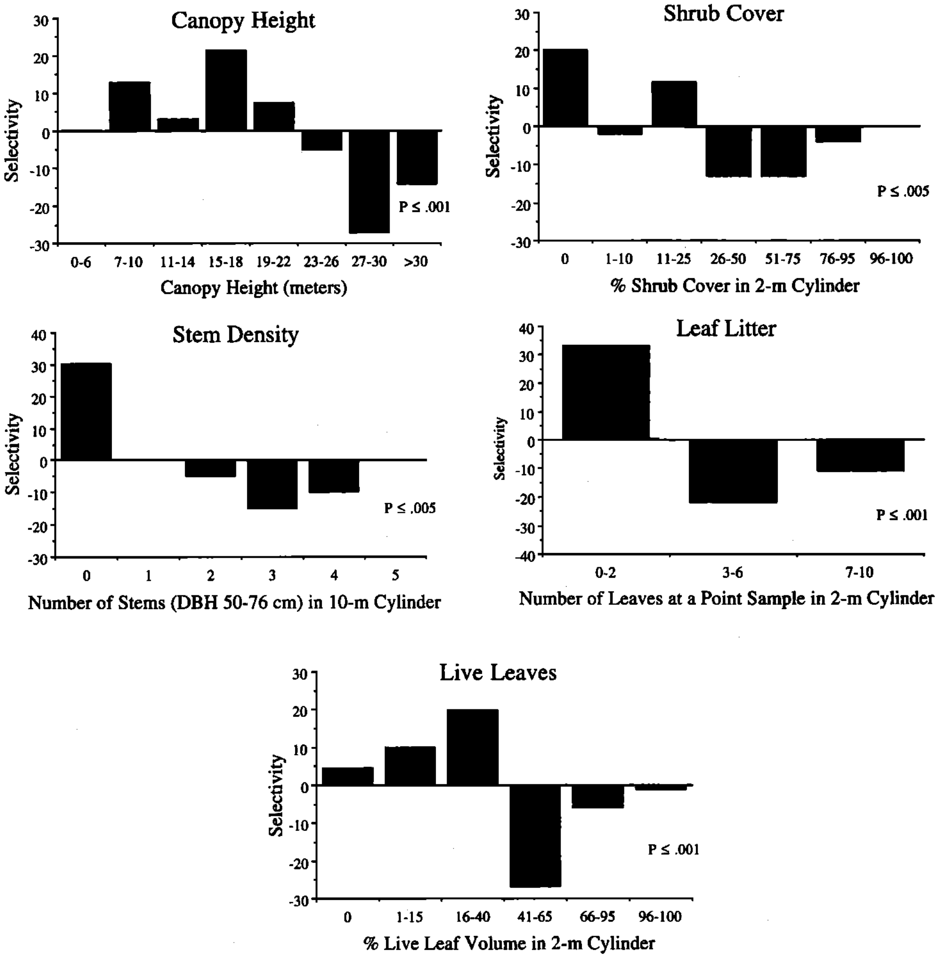


FIG. 18. Microhabitat selectivity in *Formicarius colma* in *terra firme* forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

forests (see Marra 1989). However, these differences do not really provide insight into complexity *per se*. To compare complexity, it is necessary to analyze the structural heterogeneity of each forest type. Under the assumption that the variability of the vegetation (as measured by the habitat variables) is a measure of complexity (using the general variance), we found no large differences between forest types, except for the river-edge forest, which seemed to have greater structural heterogeneity. Therefore, we agree with Terborgh (1985) that the widely assumed differences in structural habitat heterogeneity, at least as far as the understory is concerned, between temperate and tropical forests need reevaluation, and that we must look elsewhere for the major factors governing species diversity of understory birds. Although structural diversity is similar between temperate and tropical forest types, the diversity of understory birds differs greatly. Terborgh and Weske (1969), working in human-altered habitats, and Pearson (1975), studying forest birds in three Amazon localities, were also unable to explain total species diversity by habitat complexity alone.

Can unique tropical resources explain greater species diversity?—An alternative way for tropical forests to be more complex is through addition of unique resources, such as army ants, bamboo, palms, epiphytes, lianas, or year-round supplies of fruit, nectar, or suspended dead leaves. Although we did measure some of the above, the measurements and analyses conducted in this study were not designed to quantify or integrate *all* of these identifiable unique resources. Unique resources unquestionably add complexity to tropical forests and can explain the presence

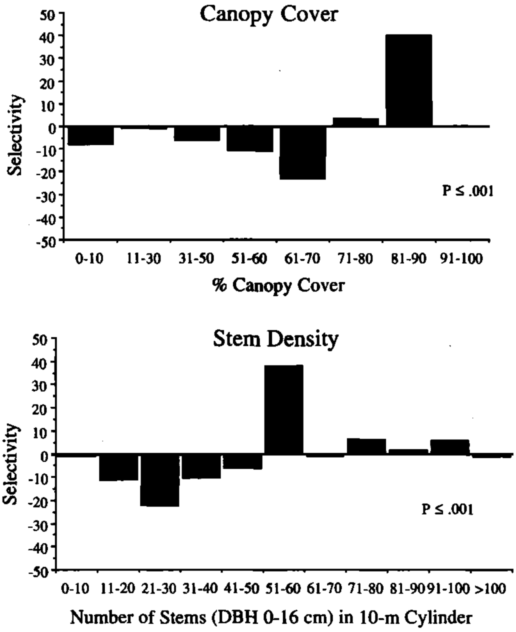


FIG. 19. Microhabitat selectivity in *Myrmeciza hemimelaena* in *terra firme* forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

of some specialized bird species (e.g., Orians 1969). However, not all the additional bird species found in tropical forests are this easily explained (Terborgh 1980a, 1985).

To compare species numbers between temperate and tropical understory forest types, it is essential to distinguish those species that are members of specialized guilds (frugivores, ant-followers, dead-leaf-searchers, vine specialists, bamboo specialists, nectarivores, and treefall specialists) from the more "generalized" species, i.e., species not obviously associated with one of these guilds added to a tropical forest by special habitats or resources. As a first approach, we examined two tropical forest types for a tropical-temperate comparison: low-lying forest (the combined river-edge and transitional forest; this combination was necessary due to difficulties in distinguishing exact boundaries between the forest types) and *terra firme* forest (Table 6). We used Foster et al. (1994) to classify species according to forest type. Of the 73 species restricted to the understory (0–5 m) of low-lying forest (Table 6), 46 (63%) can be placed into one of the above "unique tropical guilds," whereas 27 (37%) cannot. In *terra firme* forest, 20 (47%) of the 43 species (Table 6) are members of specialized guilds, whereas 23 (53%) species are not. The difference between the two forest types can be attributed to the absence from or decrease in *terra firme* forest of some of these special structural features, e.g., bamboo and vines. Nevertheless, the overall comparison to the temperate forest is dramatic. In the tropical forests, 23–27 species not associated with "tropical" resources coexist in the understory, whereas, at most only five do so at the temperate site. Such strong differences suggest that "species-packing" is much greater in the tropics. Therefore, our data provide strong support for the Klopfer and MacArthur hypothesis (1960).

Few bird species at our temperate study site are as restricted to the understory as those at the tropical site. With the exception of *Oporornis formosus,* all our temperate species spent much of their time in the subcanopy and canopy; therefore, it is even questionable that they can be classified as purely understory species (Fig. 28). Other than *O. formosus,* only *Meleagris gallopavo,* (Wild Turkey), *Pipilo erythrophthalmus* (Eastern Towhee), and *Hylocichla mustelina* (Wood Thrush) could be classified as purely understory species at Tensas, but none of these is widespread in forests there. In fact, temperate forests of North America in general have few species that could be classified as purely understory species (e.g., Ruffed Grouse, *Bonasa umbellus;* thrushes, *Catharus* spp., and Ovenbird, *Seiurus aurocapillus*). Greater vertical stratification of tropical forest birds relative to temperate zone forest birds has been proposed by many

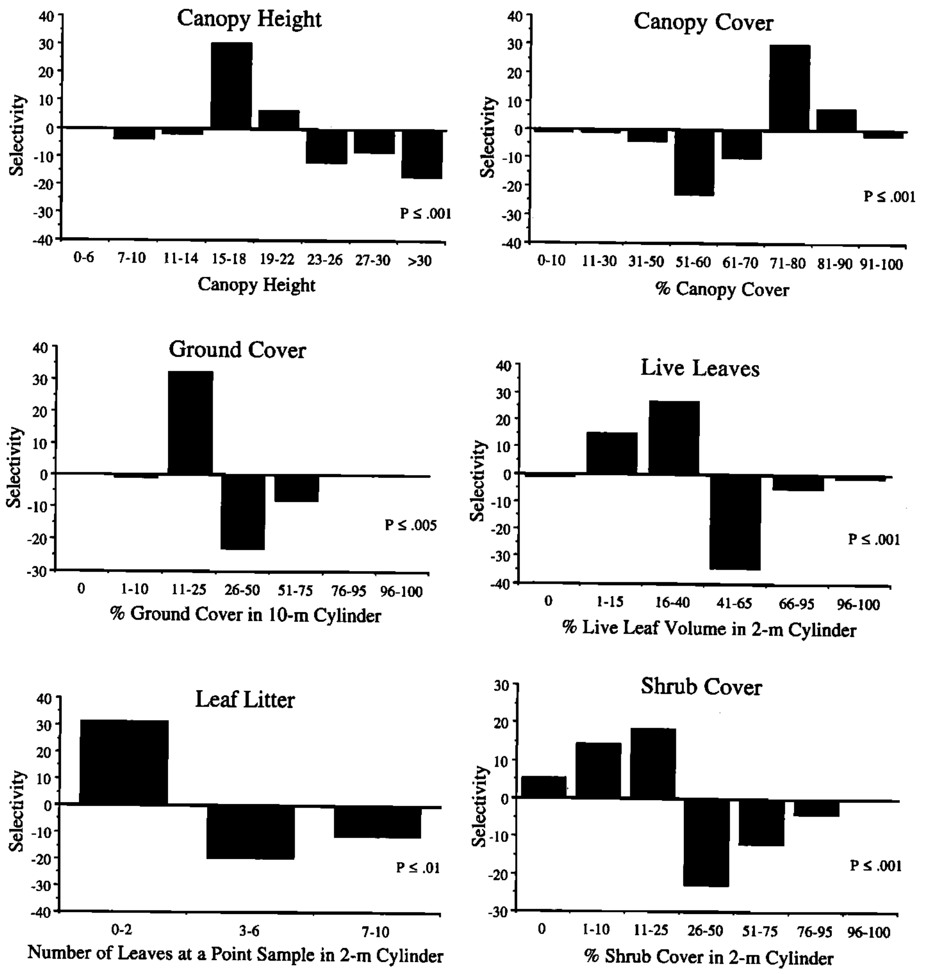


FIG. 20. Microhabitat selectivity in *Corythopis torquata* in *terra firme* forest. Positive values indicate preference (use > availability), whereas negative values indicate avoidance for the habitat variables depicted. Significance according to Kolmogorov-Smirnoff test.

investigators as one of the proximate mechanisms to explain the greater species richness of tropical forests (MacArthur 1966; Orians 1969; Terborgh and Weske 1969; Pearson 1971, 1977; Crome 1978; Terborgh 1980b; Bell 1982).

The presence of specialized guilds of birds on "unique" tropical resources (Orians 1969; Karr 1971, 1975, 1976, 1980; Lovejoy 1974; Pearson 1977; Terborgh 1980a; Remsen 1985) clearly increases species richness substantially, as illustrated above. Remsen (1985) found that most differences in species richness between tropical and temperate montane communities could be attributed to the addition of new "tropical" resources, such as the year-round availability of fruiting trees, nectar, epiphytic vegetation, vines, bamboo thickets, and suspended dead leaves. Terborgh (1980a) found that in lowland forest 34% of the "extra" tropical species were attributable to these additional guilds and attributed the remainder to greater species-packing. Terborgh's figures, however, were based upon species in the entire vertical range of a lowland forest, not just the understory, and so this could explain the differences between our calculations (63%) for low-lying forest.

Many of the special resources thought to be unique to the tropics are actually also found to a lesser degree in many forests of the southeastern United States. For instance, bamboo is present in southeastern forests, and although it has undoubtedly been drastically reduced in historical times, it has no species of birds restricted to it (with the possible exception of the virtually extinct Bachman's Warbler, *Vermivora bachmanii;* Remsen 1986). In contrast, in tropical forests,

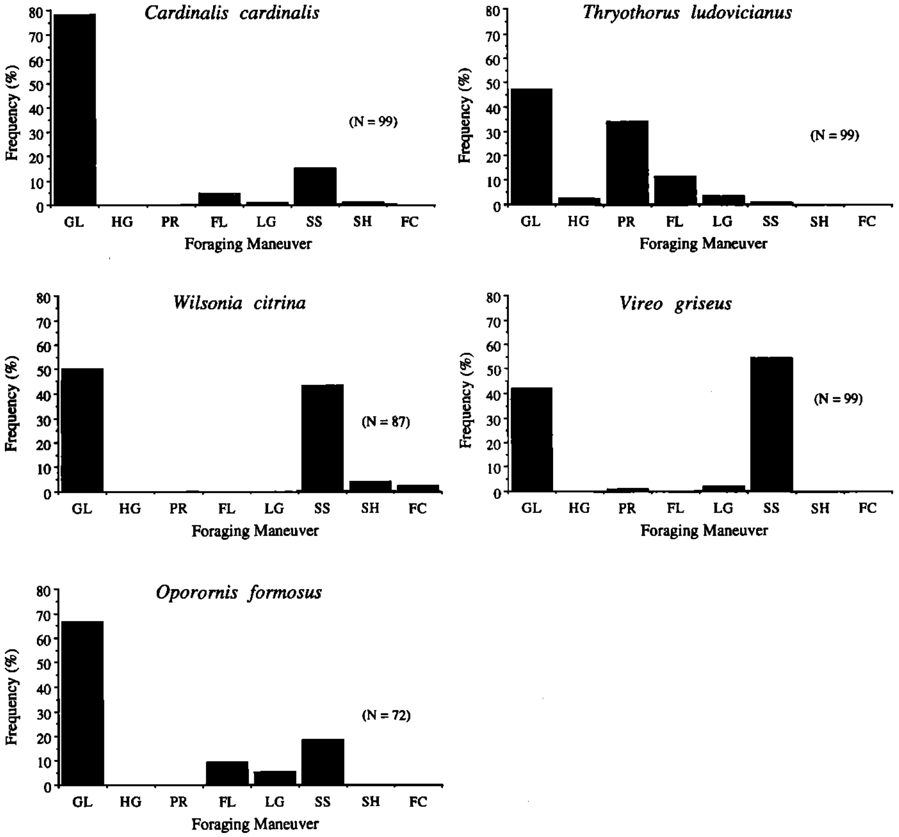


FIG. 21. The frequency (% of samples) of use of different foraging maneuvers by temperate forest species; GL = glean; HG = hang-glean; PR = probe; FL = flake; LG = leap-glean; SS = sally-strike; SH = sally-hover; FC = flutter-chase.

bamboo supports many specialized species (e.g., 16 species in Tambopata; Table 12; Kratter 1995, and in press). Two species used in this study preferred microhabitat containing bamboo but are not considered bamboo specialists. Suspended dead leaves are present in both temperate and tropical forests, although more abundantly in tropical forests, and support a number of specialists in the tropics (Remsen and Parker 1984; ≤6 species in Tambopata, Rosenberg 1990 1997). Dead-leaf foraging has been recorded in some temperate species (Remsen and Parker 1984; Remsen et al. 1989), including *T. ludovicianus* in this study, but these temperate species seem to be facultative users of dead leaves, whereas many tropical species are obligate dead-leaf foragers. Vines tangles, specialized on by some tropical species (Terborgh 1980a), were surprisingly similar in abundance between tropical and temperate forests. Interestingly, four of five temperate study species in our study preferred sites with abundant vines, whereas only one tropical study species did so. This difference is probably because our target tropical species did not include vine specialists (e.g., *Cymbilaimus fasciatus*, *Cercomacra cinerascens*, *Thryothorus* spp., and *Microbates* spp.).

The addition of new resources (structural and food related) can account for some of the increase and maintenance of higher bird species diversity in the tropics, but not for all of it. Below, we try to show that the remainder of this diversity in lowland tropics is primarily maintained by factors only secondarily related to structural habitat complexity.

Are tropical species more specialized?—Our data show that even though habitat complexity was similar in temperate and tropical forests, the target tropical species were indeed more selective and specialized in terms of microhabitat and foraging site than were the temperate species. Therefore, much of the increase in tropical species in lowland forest is due to tighter species-packing.

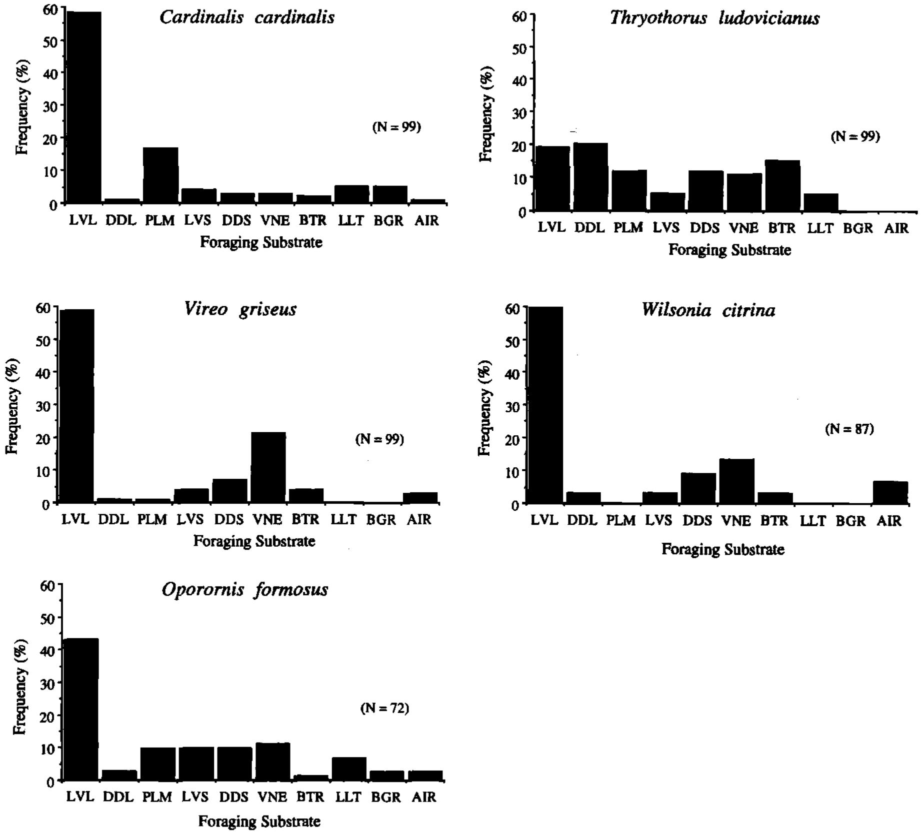


FIG. 22. The frequency (% of samples) of use of foraging substrates by temperate forest species; LVL = live leaves; DDL = dead leaves; PLM = palm; LVS = live stems; DDS = dead stems; VNE = vines; BTR = bark/trunk; LLT = leaf litter; BGR = bare ground; SWB = spider web.

The tropical species in this study specialized in a variety of ways at different levels of scale. *Myrmoborus myotherinus* was specialized at the macrohabitat level, using primarily *terra firme* forest, but was also restricted vertically in foraging height. *Myrmoborus leucophrys* was not as specialized in its selection of macrohabitat, but was more specialized in microhabitat selection, being restricted to some degree to bamboo. Thus, it was a "horizontal" specialist and was not restricted vertically. This was even more true for *H. cantator*, which was more restricted to bamboo than was *M. leucophrys*. *Formicarius analis* and *F. colma* are both "vertical" specialists in that they are entirely terrestrial. They are somewhat selective at the macrohabitat level, although not particularly selective at the microhabitat level. Both are specialized in their foraging maneuvers and substrate use relative to other target species. However, because they both forage only from the ground, the kinds of maneuvers and substrates that they can use is probably limited. The last two species, *M. hemimelaena* and *C. torquata*, neither of which are selective at the macrohabitat level, are the most generalized and most specialized (according to the general variance calculations), respectively, of all target species at the tropical sites. *Myrmeciza hemimelaena* was somewhat selective in that it preferred gaps and was fairly specialized vertically. *Corythopis torquata* can be classified as a "selecting generalist" (after Rosenzweig 1985). It was common in all three forest types; it was not selecting at the macrohabitat level, but was restricted at the microhabitat level, varying little in its selection of microhabitat variables, thus explaining its high "degree of generalization."

Overall, the temperate species were not as horizontally or vertically specialized as the tropical species. Nevertheless, some temperate species were specific in their selection of some of the microhabitat variables, whereas most were not selective of macrohabitat (although we did not use a range of sites comparable to that used in the tropics). *Cardinalis cardinalis*, *T. ludovicianus*, and to some degree *V. griseus* all expand into secondary forest habitats, and the first two species

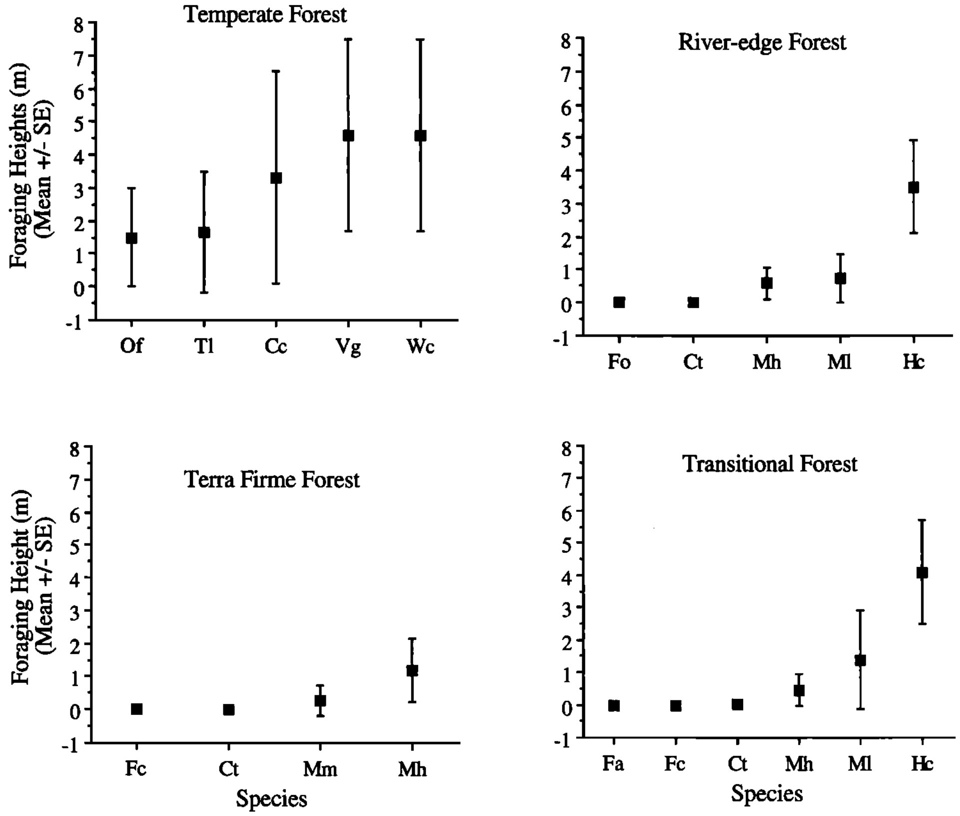


FIG. 23. Mean foraging heights with standard error bars of temperate and tropical forest species. See Table 1 for list of abbreviations.

are common in suburban habitats. However, neither of these habitat types were studied. At the microhabitat level, *V. griseus* and *T. ludovicianus* were somewhat restricted horizontally in their strong preference for microhabitat containing vines. All in all, these temperate understory species were true generalists in almost every sense of the word; they foraged throughout the vertical and to a lesser degree the horizontal range of the forest. These species were using a wide range of the habitat spectrum, unlike the tropical species.

Do tropical species overlap more in niche space?—Our calculations of niche overlap showed that the tropical species generally overlapped less among themselves than did the temperate species, but this varied depending on the foraging variable and forest type (Fig 27). Little overlap was found among tropical species in foraging height (except in *terra firme* forest), which may be a major axis of segregation among tropical species. This was not the case for temperate species. Therefore, our results do not support the hypothesis of Klopfer and MacArthur (1961) concerning the existence of greater overlap among tropical species and its importance as a mechanism contributing to the maintenance of high tropical species diversity.

We are aware of only two other studies that have attempted to quantify differences in niche metrics between guilds or communities of temperate and tropical forest birds. Stiles (1978) found that the differences in species richness between bird communities of alder forests in Washington and Costa Rica could be explained by a combination of greater specialization in foraging behavior and greater diversity of resources in the tropics. Askins (1983) found that the differences in species richness of woodpeckers in Minnesota and Guatemala was best explained by greater diversity of resources in the tropics, with some weak support for greater specialization in foraging behavior. The results of both studies are in general concordance with our results concerning the proximate mechanisms that effect species richness.

What accounts for tighter species-packing in the tropics?—We have shown that niches are more finely divided among certain tropical birds and that neither greater structural habitat com-

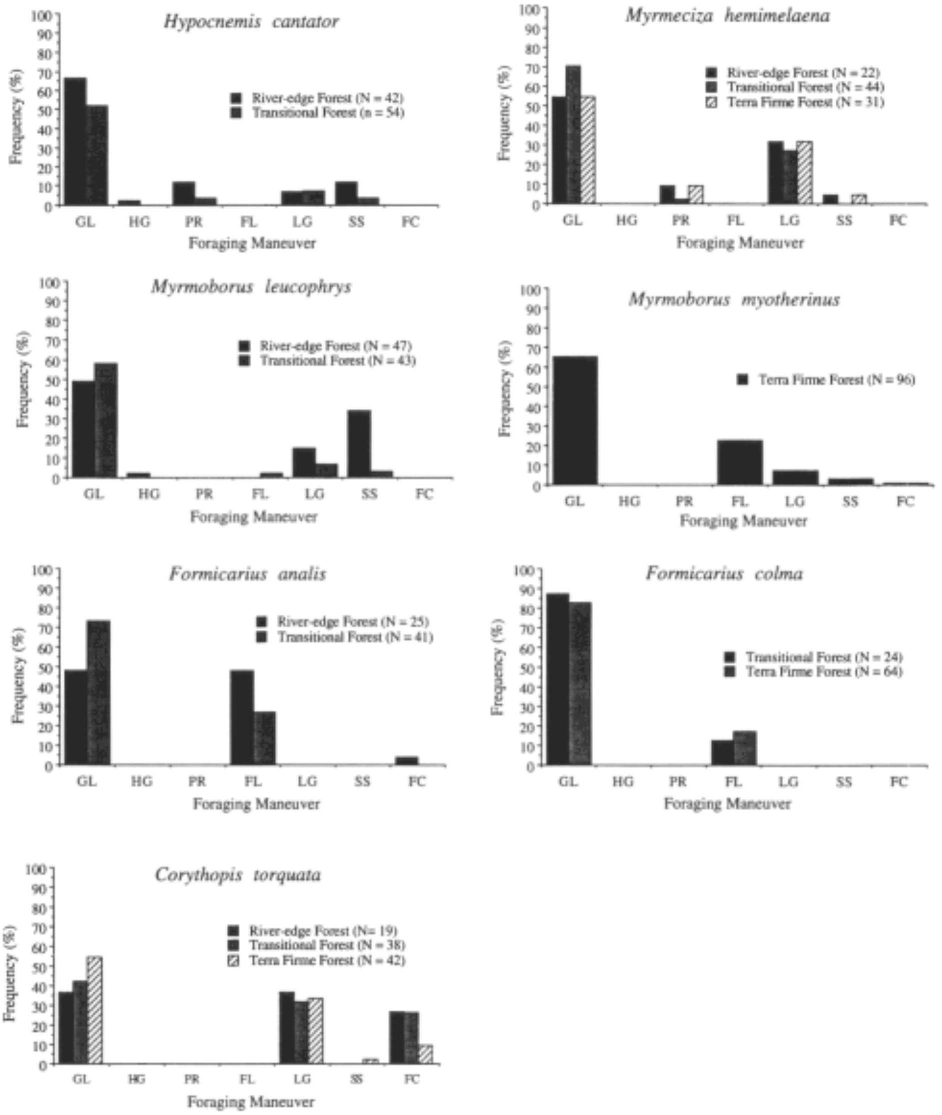


FIG. 24. The frequency (% of samples) of use of different foraging maneuvers by tropical forest species in each forest type; GL = glean; HG = hang-glean; PR = probe; FL = flake; LG = leap-glean; SS = sally-strike; SH = sally-hover; FC = flutter-chase.

plexity or greater niche overlap accounts for the high diversity at the tropical sites. The presence of "unique" tropical resources can account for many of the additional tropical species, but not all. Therefore, the remainder are able to coexist because of greater species-packing. What factors could be responsible for creating or maintaining this tighter species-packing? One hypothesis is that greater habitat and foraging-site specialization, and the higher species diversity in tropical understory birds, is maintained primarily by characteristics of the resource base (arthropods) created by greater climatic stability in the tropics (Stiles 1978). Pianka (1970) first suggested that tropical arthropods were "K-strategists" relative to their temperate counterparts. Below, we will explain how this can potentially influence habitat selection in tropical birds.

First, are tropical arthropods K-strategists, as suggested by Pianka (1970)? One characteristic of K-strategists is that they have stable populations of long-lived individuals. Unfortunately, data documenting year-round insect abundance or on insect longevity in tropical areas are meager and probably insufficient at this time for firm conclusions. Although not yet rigorously tested,

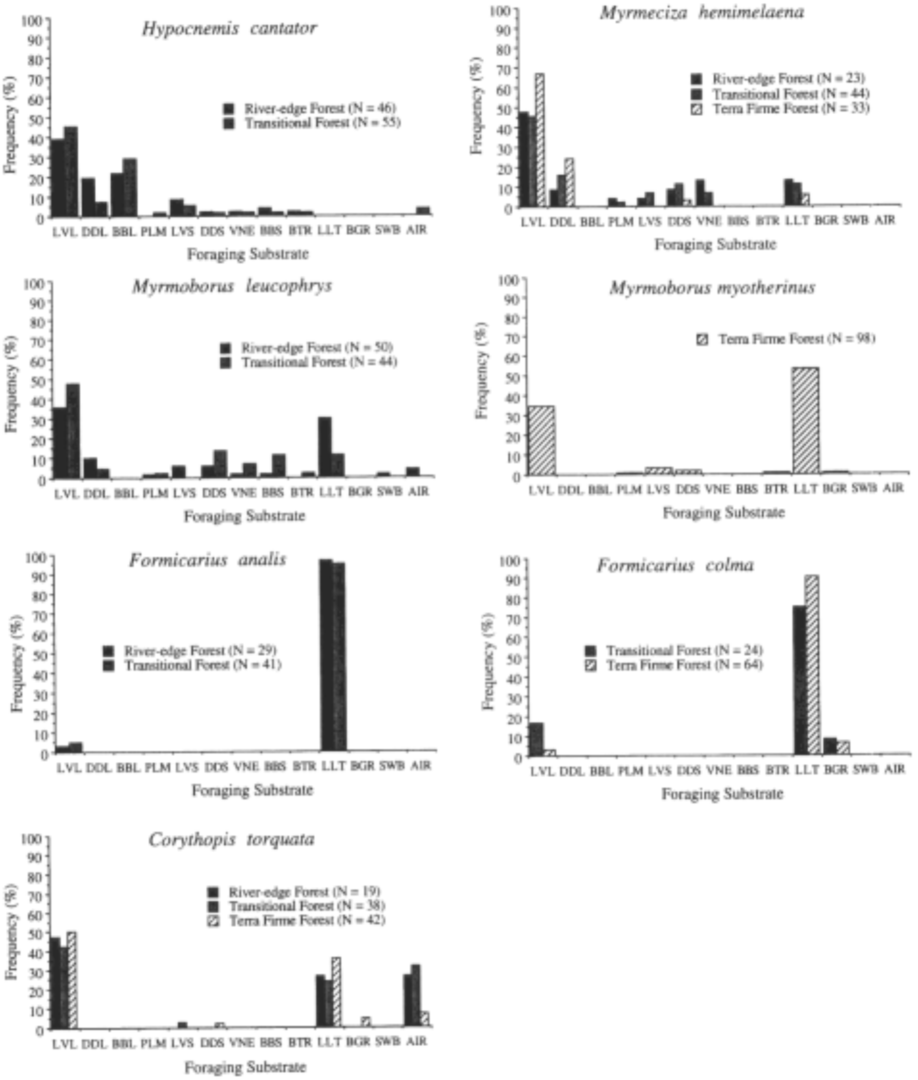
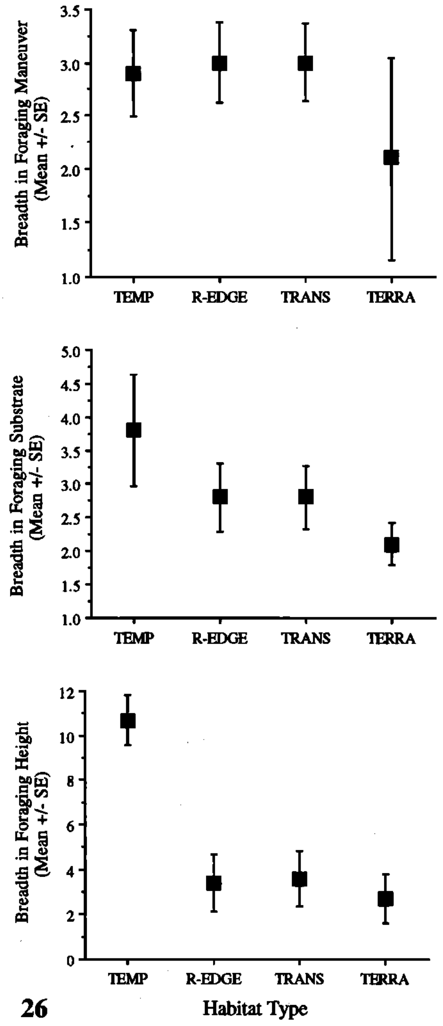


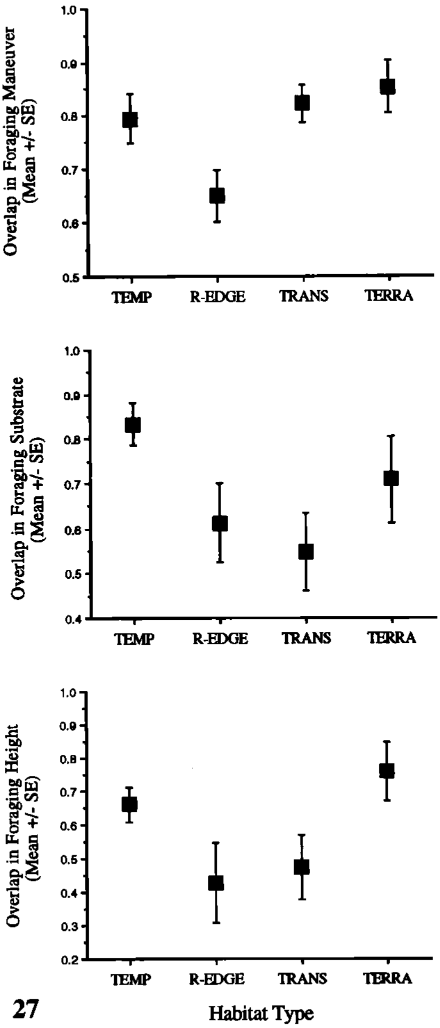
FIG. 25. The frequency (% of samples) of use of foraging substrates by tropical forest species; LVL = live leaves; DDL = dead leaves; BBL = bamboo leaves; PLM = palm; LVS = live stems; DDS = dead stems; VNE = vines; BBS = bamboo stems; BTR = bark/trunk; LLT = leaf litter; BGR = bare ground; SWB = spider web; AIR = air.

the idea maintains that tropical birds have a stable, year-round supply of insects. Recently, however, this hypothesis of a stable, year-round insect supply has been increasingly challenged (Leigh et al. 1982).

Sampling of arthropods is problematic. Many studies that have sampled insects year-round in the tropics have relied primarily on light traps and have shown some seasonality in insect abundance. Unfortunately, light traps have many shortcomings, mainly in that they only attract certain types of insects (Smythe 1982; Wolda 1978, 1982). For instance, light traps do not sample adequately two major groups used by birds, orthopterans and larval insect forms (i.e., caterpillars). These have been shown to be the major food items taken by furnariids, formicariids, and dendrocolaptids, both by field observation (Greenberg 1981; Thiollay 1988b) and by stomach analysis (mainly orthopterans; Chapman and Rosenberg 1991; Rosenberg 1997). In addition, Smythe (1982) found that the lepidopterans (adult forms), which may be effectively sampled with light traps, exhibited less seasonality than the other types of insects that can be sampled



26



27

FIG. 26. Mean (±SE) foraging maneuver, substrate and height breadths for species in each habitat type; TEMP = temperate, R-EDGE = river-edge, TRANS = transitional, TERRA = *terra firme*.

FIG. 27. Mean (±SE) foraging maneuver, substrate and height overlaps for species in each habitat type; TEMP = temperate, R-EDGE = river-edge, TRANS = transitional, TERRA = *terra firme*.

efficiently. In addition, Penny and Arias (1982) found that orthopterans make up the majority of the arthropod biomass near ground level, whereas lepidopterans do so near the canopy. Therefore, data on year-round abundance of arthropods important to birds (i.e., arthropods and lepidopterans) are inadequate at this time to test the hypothesis that tropical resource bases in the tropics are more stable. Despite these recent claims that tropical insect populations are as seasonal as temperate insect populations, extreme differences in the year-round insect abundance between tropical and temperate areas are obvious. Wolda (1988) stated that "activity seasons of tropical insects tend to be large, the percent of species active around the year higher, and the seasonal peaks less well defined, relative to counterparts at higher latitudes."

In addition to having populations lacking seasonal fluctuations, K-strategists are more likely to live longer (Pianka 1970). However, data on longevity for tropical insects is nonexistent, although lack of severe temperature fluctuations makes it seem likely that tropical insects would live longer. If so, one would predict that there would be greater selection for them to develop more anti-predator strategies, such as camouflage, mimicry systems, nocturnal behavior, and chemical defenses, than there is for temperate insects. The life-history strategies of temperate

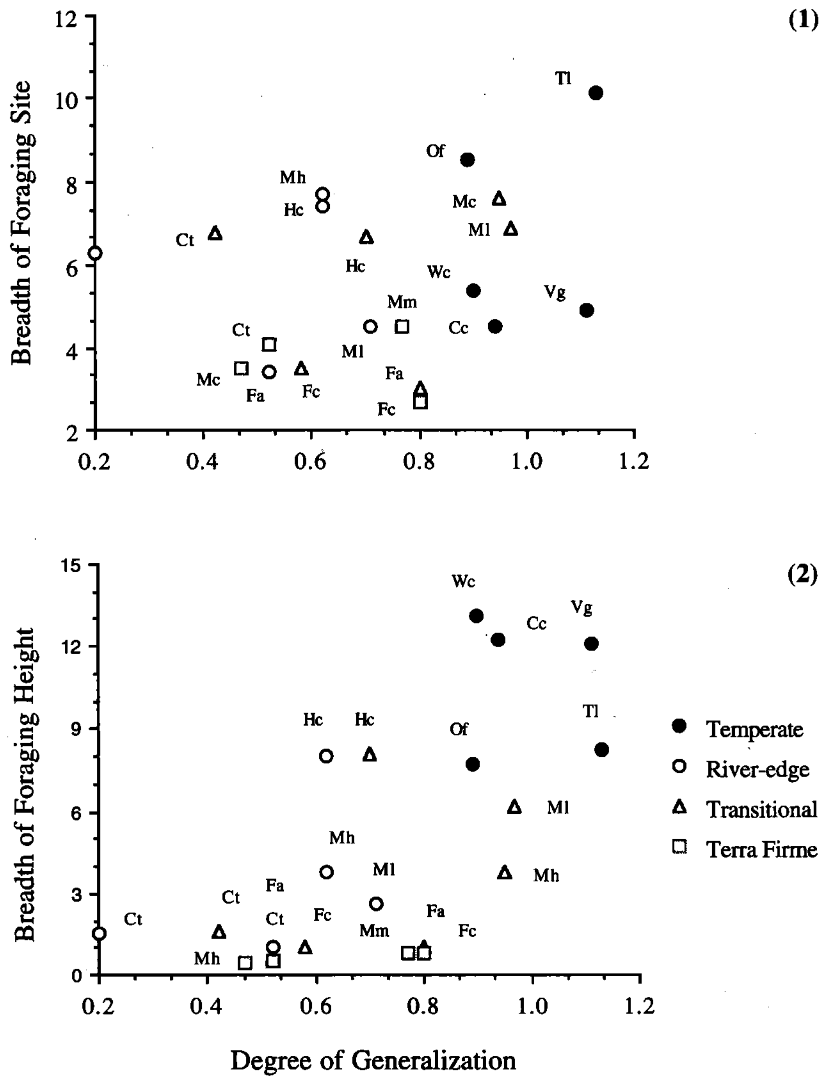


FIG. 28. 1) Breadth of foraging site (maneuver + substrate breadth for each species, see Marra 1989 for specific breadth values) and 2) breadth of foraging height vs. degree of generalization of temperate and tropical bird species. See Table 1 for list of abbreviations.

insects seem to be aimed at predator satiation (Lloyd and Dybas 1966) rather than predator avoidance.

How then would the different life-history strategies of tropical insects cause tropical birds to become more specialized and more tightly packed? It is possible that tropical birds are forced to become specialized because their resource is specialized. The key to this hypothesis would be in the lower average detectability of tropical insects compared to temperate insects (Thiollay 1988b). It may be that tropical birds have to spend more time searching substrates for prey that have developed anti-predator strategies. Support from this comes from Thiollay (1988b), who found that the mean foraging attack rate in tropical insectivorous birds was 4–6 times lower than recorded for temperate birds. Therefore, tropical birds may spend more time searching for well-hidden prey. However, it is also possible that birds are getting a better yield (i.e., larger insects; Schoener 1965; Greenberg 1981; Thiollay 1988b) from each prey item, which would mean that they do not have to feed as often, or alternatively, that metabolic demands differ between temperate and tropical birds. In any case, although there are trends in the predicted direction, our data do not demonstrate strong specialization at the foraging site by tropical birds

TABLE 6

TOTAL NUMBER OF UNDERSTORY BIRD SPECIES LISTED ACCORDING TO THEIR MOST CONSPICUOUS RESOURCE SPECIALIZATION (IF ANY) IN TWO FOREST TYPES AT THE TAMBOPATA RESERVE, SOUTHEASTERN PERU. SOME OF THESE CATEGORIES ARE NOT MUTUALLY EXCLUSIVE, AND SPECIES CAN OCCUR IN BOTH TYPES. RIVER-EDGE AND TRANSITIONAL FORESTS HAVE BEEN COMBINED AND ARE REFERRED TO AS LOW-LYING FOREST. NUMBERS OF SPECIES SUMMARIZED FROM MARRA (1989)

	Low-lying forest	Terra firme forest
Resource specialization		
Frugivores	12	7
Nectarivores	4	3
Bamboo Thickets	16	0
Vine Tangles	2	0
Treefall Gaps	2	4
Army-ant Followers	4	4
Dead-leaf searchers	6	2
Total Specialists	46 (63%)	20 (47%)
Total species without a resource specialization	27 (37%)	23 (53%)

with respect to maneuver or substrate breadths. Instead, understory tropical birds become specialized vertically (in terms of foraging height) and horizontally (in terms of microhabitat selection) relative to their temperate counterparts, and use whatever means necessary to obtain arthropods within these restricted zones. However, more data on foraging behavior combined with analyses of stomach contents is needed to conclusively determine the degree that tropical birds are specialized on specific types of arthropods.

Another factor that potentially influences the selection of habitat, either primarily, secondarily, or in combination with resources, is interspecific competition. It is possible that greater interspecific competition among the tropical study species causes them to have lower niche breadths, lower general variances, and to be overall more specialized than the temperate birds. With so many species occurring together (27 in the understory of low-lying forest), it is difficult to imagine that interspecific competition would not influence habitat selection to some degree. Recent experimental work by Robinson and Terborgh (1995) has provided further support for the importance of interspecific competition in shaping habitat selection in Amazonian birds. More data such as these are critical to increasing our understanding of what factors allow for the maintenance of high species diversity in tropical regions.

In conclusion, our comparison of the understories of temperate and tropical forests has revealed that structural differences between forest types are slight and almost certainly not sufficient to account for all differences in bird species richness. Our data support the findings of others in that the majority of additional bird species in tropical forests can be explained by two factors: (1) the presence of resources "unique" to the tropics and (2) "tighter species-packing."

ACKNOWLEDGMENTS

This work is dedicated to the memory of our dear friend and colleague Ted Parker. His dedication to and passion for understanding tropical biology inspired our own efforts. This research would not have been possible without financial support provided by the Fugler Fellowship for Tropical Vertebrate Biology, J. S. McIlhenny, and the LSU chapter of Sigma Xi. We thank Max Gunther of Peruvian Safaris S. A., Peru, and all the people at the Tensas National Wildlife Refuge for providing assistance with logistics during the research period.

J. M. Bates, R. B. Hamilton, T. A. Parker III, S. K. Robinson, K. V. Rosenberg, and G. B. Williamson provided valuable assistance with the design of the project. J. M. Bates, R. Bierregaard, J. M. Hagan, and K. V. Rosenberg made important contributions to the development of this paper. We are grateful to F. Rutledge, V. Lancaster, B. Moser, T. S. Sillett and M. P. Ayres for assistance with data analysis. Additional support was provided by the following: W. Barrow, A. P. Capparella, A. Fogg, S. J. Hackett, M. L. and P. R. Isler, G. Kinney, J. P. O'Neill, T. S. Schulenberg, P. E. Scott, and R. M. Zink.

LITERATURE CITED

ASKINS, R. A. 1983. Foraging ecology of temperate-zone and tropical woodpeckers. Ecology 64:945–956.

BARROW, W. C. 1990. Ecology of small insectivorous birds in a bottomland forest. Ph.D. dissertation, Louisiana State University. Baton Rouge, Louisiana.

BELL, H. L. 1982. A bird community of lowland rainforest in New Guinea; vertical distribution of the avifauna. Emu 82:143–162.

BROKAW, N. V. L. 1982. The definition of treefall gap and its effects on measures of forest dynamics. Biotropica 14:158–160.

CHAPMAN, A., AND K. V. ROSENBERG. 1991. Dietary relationships of four sympatric Amazonian woodcreepers (Dendrocolaptidae). Condor 93:904–915.

CODY, M. L. 1975. Towards a theory of continental species diversity. Pages 214–257 *in* Ecology and Evolution of Communities (M. L. Cody and J. M. Diamond, Eds.). Belknap Press, Cambridge, Massachusetts.

CODY, M. L. 1985. Habitat selection in the sylviine warblers of western Europe and North Africa. Pages 85–129 *in* Habitat Selection in Birds (M. L. Cody, Ed.). Academic Press, Orlando, Florida.

CROME, F. H. J. 1978. Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. Austral. J. Ecol. 3:195–212,

DE VISSCHER, M. N. 1984. Une analyse multifactorielle des relations "oiseaux-végétation" pour décrire l'habitat dans une région du piémont des Andes vénézuéliennes. Gerfaut 74:127–137.

ERWIN, T. L. 1984. Tambopata Reserved Zone, Madre de Dios, Peru: History and description of the reserve. Revista Peruviana Entomol. 27:1–8.

FITZPATRICK, J. W. 1980. Foraging behavior of Neotropical tyrant flycatchers. Condor 82:43–57.

FOSTER, R. B., T. A. PARKER III, A. H. GENTRY, L. H. EMMONS, A. CHICCHON, T. S. SCHULENBERG, L. RODRIGUEZ, G. LAMAS, H. ORTEGA, J. ICOCHEA, W. WUST, M. ROMA, J. A. CASTILLO, O. PHILLIPS, C. REYNEL, A. KRATTER, P. K. DONAHUE, AND L. J. BARKLEY. 1994. The Tambopata-Candamo Reserved Zone of Southeastern Peru: A Biological Assessment. RAP working papers 6, Conservation International, Washington, D.C.

GIBSON, R. A., BAKER, A. J., AND A. MOEED. 1984. Morphometric variation in introduced populations of the Common Myna (*Acridotheres tristis*): An application of the jackknife to principal component analysis. Syst. Zool. 33:408–421.

GREENBERG, R. 1981. Dissimilar bill shapes in tropical versus temperate forest foliage gleaning birds. Oecologia 49:143–147.

HOWELL, T. R. 1971. An ecological study of the birds of the lowland pine savanna and adjacent rain forest in northeastern Nicaragua. Living Bird 10:185–242.

JAMES, F. C., R. F. JOHNSTON, N. O. WAMER, G. J. NIEMI, AND W. J. BOECKLEN. 1984. The Grinnellian niche of the Wood Thrush. Am. Nat. 124:17–47.

JOHNSON, R. A., AND D. W. WICHERN. 1982. Applied Multivariate Statistical Analysis. Prentice Hall, Englewood Cliffs, New Jersey.

KARR, J. R. 1971. The structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41:207–233.

KARR, J. R. 1975. Production, energy pathways, and community diversity in forest birds. Pages 161–176 *in* Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research. (F. B. Golley and E. Medina, Eds.). Springer-Verlag, New York, New York.

KARR, J. R. 1976. Within- and between-habitat avian diversity in African and Neotropical lowland habitats. Ecol. Monogr. 46:457–481.

KARR, J. R. 1980. Geographical variation in the avifaunas of tropical forest undergrowth. Auk 97:283–298.

KARR, J R. 1981. Surveying birds with mist nets. Stud. Avian Biol. 6:62–67.

KARR, J. R., AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423–435.

KARR, J. R., AND K. E. FREEMARK. 1983. Habitat selection and environmental gradients: dynamics in the stable tropics. Ecology 64:1481–1494.

KIKKAWA, J., T. E. LOVEJOY, AND P. S. HUMPHREY. 1980. Structural Complexity and Species Clustering in Tropical Rainforests. Acta XVII Congressus Intern. Ornith. (1978), Pages 962–967. Berlin, West Germany.

KLOPFER, P. H., AND R. H. MACARTHUR. 1960. Niche size and faunal diversity. Am. Nat. 104:293–300.

KLOPFER, P. H., AND R. H. MACARTHUR. 1961. On the causes of tropical species diversity: niche overlap. Am. Nat. 95:223–226.

KRATTER, A. W. 1995. Bamboo specialization in Amazonian birds. Ph.D. Dissertation. Louisiana State University, Baton Rouge, Louisiana.

KRATTER, A. W. 1997. Bamboo specialization in Amazonian birds. Biotropica 29:100–110.

KUSHLAN, J. A., G. MORALES, AND P. C. FROHRING. 1985. Foraging niche relations of wading birds in tropical wet savannas. Pages 663–682 *in* Neotropical Ornithology (Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

LEIGH, E. G., A. S. RAND AND D. M. WINDSOR. (Eds.) 1982. The Ecology of a Tropical Forest. Seasonal Rhythms and Long Term Changes. Oxford Univ. Press, Oxford, U.K.

LEMMON, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314–320.

LEMMON, P. E. 1957. A new instrument for measuring forest overstory density. J. Forestry 55:667–668.

LEVEY, D. J. 1988. Treefall gaps and the distribution of understory birds and shrubs in a tropical wet forest. Ecology 69:1076–1089.

LEVINS, R. 1968. Evolution in Changing Environments. Princeton Univ. Press, Princeton, New Jersey.

LLOYD, M., AND H. S. DYBAS. 1966. The periodical cicada problem. Evolution 20:466–505.

LOVEJOY, T. E. 1974. Bird diversity and abundance in Amazon forest communities. Living Bird 13:127–191.

MACARTHUR, R. H. 1969. Patterns of communities in the tropics. Biol. J. Linn. Soc. 1:19–30.

MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.

MACARTHUR, R. H., J. W. MACARTHUR, AND J. PREER. 1962. On bird species diversity II. Prediction of bird census from habitat measurements. Am. Nat. 96:167–174.

MACARTHUR, R. H., H. RECHER, AND M. L. CODY. 1966. On the relation between habitat selection and species diversity. Am. Nat. 100:319–332.

MARRA, P. P. 1989. Habitat selection in understory birds of tropical and temperate forests. Master's Thesis, Louisiana State University, Baton Rouge, Louisiana.

MAY, R. M., AND R. H. MACARTHUR. 1972. Niche overlap as a function of environmental variability. Proc. Natl. Acad. Sci. U.S.A. 69:1109–1113.

MORSE, D. H. 1985. Habitat selection in North American parulid warblers. Pages 131–157 *in* Habitat Selection in Birds (M. L. Cody, Ed.). Academic Press, Orlando, Florida.

MOSER, E. B., W. C. BARROW, AND R. B. HAMILTON. 1990. An exploratory correspondence analysis of avian foraging behavior-habitat relationships. Pages 309–317 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Stud. Avian Biol. No. 13.

ORIANS, G. H. 1969. The number of bird species in some tropical forests. Ecology 50:783–801.

PARKER, T. A., III. 1982. Observations of some unusual rainforest and marsh birds in southeastern Peru. Wilson Bull 94:477–493.

PEARSON, D. L. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73:46–53.

PEARSON, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. Condor 77:453–466.

PEARSON, D. L. 1977. Ecological relationships of small antbirds in Amazonian bird communities. Auk 94: 283–292.

PENNY, N. D., AND J. R. ARIAS. 1982. Insects of an Amazon Forest. Columbia Univ. Press, New York, New York.

PIANKA, E. R. 1970. On r- and k- selection. Am. Nat. 104:592–596.

PIANKA, E. R. 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. U.S.A. 71:2141–2145.

REMSEN, J. V., JR. 1985. Community organization and ecology of birds of high elevation humid forest of the Bolivian Andes. Pages 733–756 *in* Neotropical Ornithology (Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

REMSEN, J. V., JR. 1986. Was Bachman's Warbler a bamboo specialist? Auk 103:216–219.

REMSEN, J. V., JR. 1990. Community ecology of Neotropical kingfishers. Univ. Calif. Publ. Zool. 124:1–116.

REMSEN, J. V., JR., M. ELLERMAN, AND J. COLE. 1989. Dead-leaf searching by the Orange-crowned Warbler in Louisiana in winter. Wilson Bull. 101:645–648.

REMSEN, J. V., JR., AND D. A. GOOD. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113:381–398.

REMSEN, J. V., JR., AND T. A. PARKER III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15:223–231.

REMSEN, J. V., JR., AND T. A. PARKER III. 1984. Arboreal dead-leaf-searching birds of the Neotropics. Condor 86:36–41.

REMSEN, J. V., JR., AND S. K. ROBINSON. 1990. A classification scheme of avian foraging behavior in terrestrial habitats. Pages 144–160 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison C. John Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Stud. Avian Biol. No. 13.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

ROBINSON, S. K., AND J. TERBORGH. 1995. Interspecific aggression and habitat selection by Amazonian birds. J. Animal Ecology 64:1–11.

ROSENBERG, G. H. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. Condor 92:427–443.

ROSENBERG, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: Measuring resource availability and use. Pages 360–368 *in* Avian Foraging: Theory, Methodology and Applications. (Morrison, M. L., C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Stud. Avian Biol. No. 13.

ROSENBERG, K. V. 1997. Ecology of dead-leaf-searching specialists and their contribution to Amazonian bird diversity. Pages 673–700 *in* Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithol. Monogr. No. 48.

ROSENZWEIG, M. L. 1985. Some theoretical aspects of habitat selection. Pages 517–540 *in* Habitat Selection in Birds (M. L. Cody, Ed.). Academic Press, Orlando, Florida.

SAS INSTITUTE. 1985. SAS User's Guide: Statistics, version 5 edition. SAS Institute, Inc., Cary, North Carolina.

SAS INSTITUTE. 1995. JMP: Statistics and Graphics Guide, version 3.1. SAS Institute, Inc., Cary, North Carolina.

SCHEMSKE, D. W., AND N. BROKAW. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology 62:938–945.

SCHOENER, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19:189–213.

SILVA, J. M. C. DA, AND R. CONSTANTINO. 1988. Aves de um trecho de mata no baixo Rio Guamá —uma reanálise: riqueza, raridade, diversidade, similaridade e preferências ecológicas. Bol. Mus. Paraense Emilio Goeldi, sér. Zool. 4:201–210.

SMITH, A. P. 1973. Stratification of temperate and tropical forests. Am. Nat. 107:671–683.

SMYTHE, N. 1982. The seasonal abundance of night-flying insects in a Neotropical forest. Pages 309–318 *in* The Ecology of a Tropical Forest. Seasonal Rhythms and Long Term Changes (Leigh, E., Jr., A. S. Rand, and D. Windsor, Eds.). Oxford Univ. Press, Oxford, U.K.

STILES, E. W. 1978. Avian communities in temperate and tropical alder forests. Auk 80:276–284.

TERBORGH, J. W. 1980a. Causes of Tropical Species Diversity. Actis Congr. Int. Ornithol., XVII (1978): 955–961. Berlin, West Germany.

TERBORGH, J. 1980b. Vertical Stratification of a Neotropical Forest Bird Community. Actis Congr. Int. Ornithol. XVII (1978):1005–1012. Berlin, West Germany.

TERBORGH, J. 1985. Habitat Selection in Amazonian Birds. Pages 311–338 *in* Habitat Selection in Birds (M. L. Cody, Ed.). Academic Press, Orlando, Florida.

TERBORGH, J. W., AND J. S. WESKE. 1969. Colonization of secondary habitats by Peruvian birds. Ecology 50:765–782.

TERBORGH, J. W., AND S. K. ROBINSON. 1986. Guilds and their utility in ecology. Pages 65–90 *in* Community Ecology: Pattern and Process (J. Kikkawa and D. J. Anderson, Eds.). Blackwell Scientific Publications, Oxford, U.K.

TERBORGH, J. W., J. W. FITZPATRICK, AND L. H. EMMONS. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. Fieldiana (Zool.) 21:1–29.

THIOLLAY, J. M. 1988a. Diversité spécifique et coexistence en forêt tropicale: L'occupation des mileux par une guilde d'oiseaux insectivores en Guyane. Rev. Ecol. (Terre Vie) 43:59–92.

THIOLLAY, J. M. 1988b. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17–30.

WILLSON, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017–1029.

WILLSON, M. F., S. H. ANDERSON, AND B. G. MURRAY. 1973. Tropical and temperate bird species diversity: Within-habitat and between-habitat comparisons. Carib. J. Sci. 13:81–90.

WILLSON, M. F., AND D. J. MORIARTY. 1976. Bird species diversity in forest understory: analysis of mist-net samples. Oecologia 25:373–379.

WOLDA, H. 1978. Fluctuations in abundance of tropical insects. Am. Nat. 112:1017–1045.

WOLDA, H. 1982. Seasonality of Homoptera on Barro Colorado Island. Pages 319–330 *in* The Ecology of a Tropical Forest. Seasonal Rhythms and Long Term Changes (Leigh, E., Jr., A. S. Rand, and D. Windsor, Eds.). Oxford Univ. Press, Oxford, U.K.

WOLDA, H. 1988. Insect seasonality: Why?. Ann. Rev. Ecol. Syst. 19:1–18.

WUNDERLE, J. M., JR., A. DIAZ, I. VELAZQUEZ, AND R. SCHARRON. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bull. 99:22–37.