

WILEY



---

Foraging Ecology of Temperate-Zone and Tropical Woodpeckers

Author(s): Robert A. Askins

Source: *Ecology*, Vol. 64, No. 4 (Aug., 1983), pp. 945-956

Published by: Wiley on behalf of the Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1937215>

Accessed: 17-05-2017 20:55 UTC

## REFERENCES

Linked references are available on JSTOR for this article:

[http://www.jstor.org/stable/1937215?seq=1&cid=pdf-reference#references\\_tab\\_contents](http://www.jstor.org/stable/1937215?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



Wiley, Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to *Ecology*

## FORAGING ECOLOGY OF TEMPERATE-ZONE AND TROPICAL WOODPECKERS<sup>1</sup>

ROBERT A. ASKINS<sup>2</sup>

*Bell Museum of Natural History, Department of Ecology and Behavioral Biology,  
University of Minnesota, Minneapolis, Minnesota 55455 USA*

**Abstract.** The foraging behavior of 11 species of woodpeckers in Guatemala, Maryland, and Minnesota was studied in order to test the seasonal stability hypothesis. This hypothesis predicts that specialization and species richness should be no greater for tropical wood-excavators than for those in the temperate zone because wood-excavators in both regions are buffered against seasonal change. Niche breadth values for six variables that describe foraging methods and perches were calculated by two methods. Unweighted niche breadth values were similar for tropical and temperate woodpeckers for all variables except foraging technique; in this case the temperate species are more specialized. With weighted niche breadth values temperate species are more specialized for two variables and less specialized for two others. Thus there is no consistent tendency for tropical species to be more specialized.

However, the excavating guild includes twice as many species in Guatemala as in either of the northern study sites. Two of the three "additional" species in Guatemala use a configuration of foraging methods and perches not used by northern woodpeckers. Hence the larger number of tropical woodpecker species can be attributed partly to the greater range of resources available in the structurally complex rain forest.

**Key words:** Central America; community structure; deciduous forest; foraging behavior; guild; latitudinal gradient; rain forest; seasonality; specialization; species diversity; woodpecker.

### INTRODUCTION

It is generally true that more species of birds coexist per unit area in Central America than in temperate North America (Cook 1969, Tramer 1974); many foraging guilds in Central America have two to four times as many species as their temperate-zone counterparts (Orians 1969, Karr 1971, 1976, Stiles 1978). Some taxonomic groups and foraging guilds do not follow this trend, but usually these exceptions are explained in terms of biogeographical history (Simpson 1964) or the absence of certain habitats in the tropics (Cook 1969). An intriguing exception that may have broader ecological significance involves woodpeckers. Deciduous forests in the northeastern United States have nearly the same number of species of woodpeckers as mature rain forests in Central America. The former have four to six species (Williams 1947, Stewart et al. 1952, Gamboa and Brown 1976, Criswell et al. 1979, Stapleton 1979), while the latter have five to seven (Eisenmann 1952, Davis and Moroney 1953, Howell 1957, Slud 1960, Andrlé 1967). This similarity is particularly noteworthy because woodpeckers comprise a relatively discrete ecological group with a foraging specialization (drilling into bark and wood) not shared by other groups of North American birds. As an apparent exception to the pattern of increasing species richness toward the equator, woodpeckers might provide a clue to why the pattern exists.

Several hypotheses attempt to explain latitudinal gradients in species richness (Pianka 1966, Whittaker 1972). Most emphasize evolutionary history, environmental heterogeneity, environmental disturbance, predation, or productivity, factors that do not obviously affect woodpeckers differently from other organisms. However, one hypothesis, the seasonal stability hypothesis (Klopfer 1959, Recher 1971), suggests why woodpeckers should be exceptional. The important factor in this hypothesis is seasonal change in the environment; as I will discuss below, woodpeckers are exceptionally well buffered against seasonal changes in both food supply and weather.

According to the seasonal stability hypothesis, the degree of seasonal fluctuation in the environment controls the degree of specialization, and this, in turn, controls species richness. In an environment with relatively little seasonal change, such as a tropical rain forest, certain resources are dependable throughout the year, and species can become narrowly specialized in their foraging behavior. Many specialists can coexist even if competitive equilibrium (Huston 1979) is achieved. In a highly seasonal environment, such as a temperate-zone forest, most species are forced to be generalists, since they must use different resources at different seasons, regardless of whether they migrate to a different region or over-winter in the greatly altered local environment. If competitive equilibrium is approached or achieved, relatively few of these generalists can coexist. Their resource needs will overlap much more than do those of specialized species in the tropics and, as a result, competitive exclusion will occur more frequently.

<sup>1</sup> Manuscript received 10 August 1981; revised 24 June 1982; accepted 29 June 1982.

<sup>2</sup> Present address: Department of Zoology, Connecticut College, New London, Connecticut 06320 USA.

TABLE 1. Description of study sites.

Locality	Coordinates	Average annual precipitation (mm)	Average temperature (°C)			Elevation (m)	References
			Warmest month	Coolest month			
Tikal National Park, Guatemala	89°38'W, 17°13'N	1376	April: 26	January: 21		250	Smithe 1966, Cant 1978
Chesapeake Bay Center for Environmental Studies, Maryland	76°33'W, 38°53'N	1173	July: 25	January: 2		17	Higman 1968
Chain of Lakes Park, Minnesota	93°07'W, 45°09'N	682	July: 23	January: -11		273	Baker and Strub 1965, Baker et al. 1967

Support for this hypothesis comes from documentation of positive correlations between seasonal stability and species richness (Patrick 1966, Sanders 1969, Porter 1972), and from evidence that tropical species are more specialized than their temperate-zone ecological counterparts (Stiles 1978, Jeanne 1979, Emmons 1980). However, many studies show no correlation or a negative correlation between seasonal stability and species richness. Many of these cases involve comparisons within a single climatic zone (Orians 1969, Whittaker 1972, Pianka et al. 1979), where there are no consistent latitudinal gradients in species richness and where the large differences in seasonal stability that might be necessary for geographical variation in degree of specialization do not exist (Tramer 1974, Rabenold 1979). Other cases involve communities in which interspecific competition is apparently not important (Wiens 1977, Connell 1978, Rabenold 1978). The seasonal stability hypothesis assumes that competition among species limits the number of species that can coexist, so it would not apply to these communities. However, it may apply to the woodland bird communities that are the focus of this study. Although analysis of foraging guild structure indicates that some woodland bird communities are not close to competitive equilibrium (Rabenold 1978), perturbation experiments provide convincing evidence that competition is important for some woodland birds (Davis 1973, Williams and Batzli 1979a, Höglstedt 1980, Minot 1981).

The seasonal stability hypothesis is relevant to woodpeckers because they may be relatively unaffected by seasonal change. Roost and nest cavities buffer them against seasonal changes in weather (Askins 1981b), and those woodpecker species that feed on bark insects have a dependable source of food throughout the year. The density of invertebrates in synthetic logs placed in an English forest was similar in winter and summer (Fager 1968). Moreover, many species of wood-boring larvae require 1–3 yr to mature (Graham and Knight 1965), so these insects are present (and often represented by several instars) at any time of the year. Carpenter ants are also available throughout the year to birds that are capable of excavating deep into wood (Sudd 1967). Hence wood-

peckers may have a relatively stable food supply in the temperate zone as well as in the tropics.

According to the seasonal stability hypothesis, if seasonal change is equivalent for tropical and temperate woodpeckers, then they should be similar with regard to foraging specialization and species richness. Since woodpeckers do appear to have similar levels of species richness in the two climatic zones, the crucial question is whether tropical and temperate species are specialized to the same extent. The seasonal stability hypothesis would not be tenable (at least as it applies to woodpeckers) if the following two conditions are met: (1) tropical woodpeckers have smaller niche breadths than temperate woodpeckers; (2) this contrast in niche breadths is at least as great as analogous contrasts reported in other studies of tropical and temperate birds, such as Stiles' (1978) study of the leaf-gleaning guild.

## STUDY AREAS AND METHODS

### Study areas

*Tikal National Park, Guatemala.*—This 576-km<sup>2</sup> park in the northern Petén (Table 1) is contiguous with a large expanse of relatively undisturbed forest that stretches northward beyond the Mexican border. The 596-ha study area was located within the major Mayan ruins of Tikal, in the area within 2–3 km of the Great Plaza. The ruins are located on a ridge covered with "high forest" (Smithe 1966). The forest canopy is higher than 30 m, with some emergent trees >50 m tall. Lundell (1937) gives a detailed description of the vegetation of northern Petén, including the high forest ("climax formation") characteristic of the Tikal ruins.

According to Holdridge's (1956) classification, the forest at Tikal is intermediate between the tropical-dry-forest and low-subtropical-moist-forest categories. The effects of the dry season are moderated by frequent morning fogs that leave the vegetation wet (Smithe 1966). Only a small proportion of the canopy is bare during the dry season and most trees are covered with vines and epiphytes.

Secondary forest (Lundell 1937) is largely limited to small areas near the park headquarters and main ruins.

The understory has been removed near some ruins, resulting in a park-like habitat. On the edge of the study area there are large expanses of escobal, a low, swampy forest dominated by escoba palm (*Cryosophila argentea*) and botan palm (*Sabal morrisiana*) (Lundell 1937). The various habitats are represented in the following proportions on my study area: high forest: 80%; secondary forest: 6%; park-like areas: 5%; escobal: 9%.

I worked at Tikal for 3 mo during the wet season (18 June–14 September 1977) and 2 mo during the dry season (12 January–11 March 1978).

*Chain of Lakes Park, Anoka County, Minnesota, USA.*—The 127-ha study area was located on a low wooded ridge between Rice and Reshanau lakes in Chain of Lakes Park (Table 1). The woods are mature deciduous forest with a canopy 20–25 m high. Parts of the forest have been opened by windstorms and Dutch elm disease. The dominant trees are *Tilia americana*, *Celtis occidentalis*, *Ulmus americana*, *Fraxinus pennsylvanica*, and *Quercus borealis*. The thick understory consists primarily of the shrubs *Sambucus pubens* and *Xanthoxylum americanum* and a ground cover of *Laportea canadensis* and *Hydrophyllum virginianum*. The deciduous forest covers 45% of the study area; 14% is cattail marsh and 41% is lawn with scattered trees or open meadow.

I made frequent (usually weekly) visits to the Chain of Lakes study area between 19 January 1975 and 25 October 1979, except for the periods when I was in Maryland and Guatemala, and from 17 June to 13 September 1975. Daily visits were made between 14 June and 1 September 1976.

*Chesapeake Bay Center for Environmental Studies, Anne Arundel County, Maryland, USA.*—The Java Farm Woods is a tall deciduous forest in the Rhode River watershed (Table 1). The main woods, which has a canopy ≈30 m high, is surrounded by large areas of young second-growth woods. Mature forest comprises 46% of the 170-ha study area, whereas young secondary deciduous forest accounts for 41% and open habitats (meadow, agricultural fields, and lawns) account for 13%. Higman (1968) gives a detailed description of the history and vegetation of the area.

I spent two periods observing woodpeckers at this site: 9 October 1978–3 January 1979; and 28 February–9 March 1980.

#### Study species

Only those woodpeckers that have a seasonally stable food source would be expected to have similar levels of specialization in the tropics and temperate zone, so only woodpeckers that excavate into wood to extract wood-boring larvae and ants are considered in this study. At the northern sites three species of woodpeckers: Common Flicker (*Colaptes auratus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), and Yellow-bellied Sapsucker (*Sphyrapicus vari-*

*ius*), spend little or no time excavating for insects; instead they use different methods of foraging such as eating fruit and nuts, sapsucking, and terrestrial ant-eating (Lawrence 1966, Tate 1973, Jackson 1976, Moskovits 1978). These species were therefore excluded from the study. Although some tropical woodpeckers forage primarily by gleaning, probing, and eating fruit (Skutch 1969, Short 1970), the published information on the tropical species I studied was not detailed enough to conclude that particular species should be excluded from the study *a priori*.

At my three study sites the excavating guild does not include birds other than woodpeckers. Woodcreepers (Dendrocolaptidae) and the furnariid *Xenops minutus* occasionally dig insects out of wood (Skutch 1969, R. A. Askins, personal observation), but they primarily forage in other ways (Willis 1966, Skutch 1969, Feduccia 1970). The White-breasted Nuthatch (*Sitta carolinensis*), which has been reported “tapping and hammering” (Willson 1970), forages primarily by hammering open seeds and acorns, and by probing into bark crevices (Bent 1948, Williams and Batzli 1979b).

I studied the following species in Guatemala: Golden-olive Woodpecker (*Piculus rubiginosus*), Chestnut-colored Woodpecker (*Celeus castaneus*), Lineated Woodpecker (*Dryocopus lineatus*), Golden-fronted Woodpecker (*Melanerpes aurifrons*), Black-cheeked Woodpecker (*M. pucherani*), Smoky-brown Woodpecker (*Veniliornis fumigatus*), and Pale-billed Woodpecker (*Campephilus guatemalensis*). In both Maryland and Minnesota I studied the Pileated Woodpecker (*Dryocopus pileatus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Hairy Woodpecker (*Dendrocopos villosus*), and Downy Woodpecker (*D. pubescens*). I found that Red-bellied and Golden-fronted woodpeckers did not excavate frequently enough to be included in the excavating guild, so they are not included in the analysis below.

#### Field techniques

I used prescribed routes to cover each study area, usually watching woodpeckers in the 4–5 h after dawn and the 2 h before dusk. When I encountered a woodpecker, I recorded its behavior for 5 min or until I lost sight of the bird. This interval is the observation period. A spotting scope or binoculars were used to observe the bird, and a cassette recorder was used to record data. The species, sex, and age (immature vs. adult) were noted, and I measured the time an individual spent foraging in each tree or shrub and on each branch within a tree or shrub. Information about the following six variables was recorded for all of the foraging sites used by a particular woodpecker during the observation period:

- 1) Height above ground. A distance finder (Rangematic or Ranging 120, Ranging Incorporated, East Rochester, New York, USA) and an angle finder were

used to determine the height (to within 1 m) at which an individual first foraged on each separate tree or shrub.

2) Size of branch. The bill of the bird was used as a standard to estimate the diameter of the branch upon which the bird was foraging.

3) Type of wood. Each branch used by the woodpecker was classified as dead or alive.

4) Habitat. I marked the initial location of each woodpecker on a detailed map of the study area. The map was drawn from an aerial photograph for the Minnesota site, and from detailed topographical maps for the Maryland and Guatemala sites (Carr and Hazard 1961). A grid 100 × 100 m was superimposed on each map and each grid square was characterized as being predominantly mature forest, second-growth forest, or open habitat (e.g., park-like area, meadow, agricultural field). These broad categories facilitated comparisons of the tropical and temperate sites.

5) Movement pattern. The number of hops in different directions within a tree (i.e., up, down, around a branch, toward the trunk, away from the trunk) were counted.

6) Foraging techniques. The length of separate foraging bouts was timed and each bout was assigned to one of the following categories:

- a) excavating: digging beneath the bark surface for food;
- b) probing into excavation: inserting bill or tongue into excavations created by tapping;
- c) probing: inserting the bill or tongue into cracks or crevices, or picking insects off the bark surface;
- d) gleaning: picking insects from leaf surfaces;
- e) fruit-eating: eating nuts or fruit.

Similar variables have been used successfully in comparisons of the foraging behavior of different species of woodpeckers or of males and females of a single woodpecker species (Selander 1966, Jackson 1970, Alatalo 1978).

#### *Quantitative analysis of the guild*

The primary prediction of this study is that tropical and temperate-zone woodpeckers specialize in their foraging behavior to the same extent. A measure of foraging specialization, or niche breadth, is therefore required. Levins' (1968) formula

$$B = 1/[n \sum p_i^2] \quad (1)$$

is a simple, easily interpretable measure of how evenly individuals of a particular species use a range of foraging methods and perches. For each variable (e.g., foraging height, branch diameter) arbitrary resource states are defined. For example, I classified foraging heights into nine resource states (0–1 m, 1–3 m, 3–5 m, 5–10 m, etc.). Niche breadth ( $B$ ) is calculated for each variable separately. The proportion of foraging time a species spends foraging at resource state  $i$  is  $p_i$ , and  $n$  is the total number of resource states for the

variable under consideration. Values range from 1, for equal use of all resource states, to  $1/n$  for specialization on one resource state.

In order to understand the pattern of relationships among species, I calculated niche overlap values and used multivariate analysis. The niche overlap value for two species is seldom a good indication of competition (Colwell and Futuyma 1971, Abrams 1980), but it can be a useful description of similarity in resource use. An index of proportional similarity (Schoener 1970)

$$C_{xy} = 1 - \frac{1}{2}(\Sigma |p_{xi} - p_{yi}|) \quad (2)$$

indicates the amount of overlap between two species in utilization of resource states for a particular variable. The proportion of foraging time species  $x$  spends at resource state  $i$  is  $p_{xi}$ , while the proportion for species  $y$  is  $p_{yi}$ . Values range from 0 (no overlap in resource use) to 1 (complete overlap). Abrams (1980) argues that this index more closely approximates the notion of "overlap" than other commonly used indices (including those that consider availability of resources and density of competitors), and thus is superior for descriptive purposes.

Niche overlap values do not clearly reveal the overall structure of the guild. The relationships of different coexisting species are described by the six resource variables, and these relationships might be apparent if points in six-dimensional space could be visualized. Multivariate analyses (principal component analysis and discriminant analysis) were used to collapse the number of dimensions from six to two so that the relationships among the species could be presented graphically (Nie et al. 1975). Both of these techniques require continuous variables, however, and four of the six variables (wood type, habitat, movement pattern, and foraging technique) are categorical. I therefore used the time spent in each resource state to make a set of new variables for these analyses. The time individual birds spent in resource states was measured in seconds, so all of the new variables are continuous. Preliminary analysis indicated that many of these resource states are interdependent in regular ways; for instance, a woodpecker using one small-branch category tends to use other small-branch categories. I therefore simplified the resource states to increase the power of the multivariate techniques to show relationships among species rather than relationships among resource states. Data for each variable (other than foraging technique) were categorized into two resource states (e.g.,  $\leq 10$  m and  $> 10$  m for foraging height). Foraging technique is too complex to deal with in this manner, so five resource states (short excavation, long excavation [ $> 50$  s], surface probing, probing into excavations, and fruit-eating) were considered. The proportion of time each individual spent with respect to each of these simplified resource states (new variables) was used in the analyses. With the exception of foraging technique, only one resource state for each vari-

TABLE 2. Total observation time and total number of independent observations for woodpecker species observed at three study sites.

Sample measure	Guatemala						Maryland				Minnesota				
	Golden-olive	Chestnut-colored	Lineated	Golden-fronted	Black-cheeked	Smoky-brown	Pale-billed	Pileated	Red-bellied	Hairy	Downy	Pileated	Red-bellied	Hairy	Downy
Total time (min)	372	96	624	480	382	228	1014	312	606	228	609	216	102	1044	978
No. of observations	79	28	151	140	123	66	237	51	213	60	180	32	24	299	251

able was needed, since the two resource states are dichotomous and use of both proportions would be redundant. Consequently 10 resource states (5 for foraging technique and 1 for each of the other 5 original variables) were used.

The use of proportions violates the assumption of normality for principal component and discriminant analysis, but these multivariate techniques are being used solely for ordination (graphical display), not for tests of statistical significance. They are robust with respect to frequency distribution when used for this purpose. An arcsine transformation was used to normalize the distribution of the proportions, but this did not change the basic pattern of interspecific relationships derived from untransformed proportions. Moreover, two different types of multivariate analysis were used to substantiate the robustness of the general pattern of interspecific relationships.

The two-sample *t* test and the chi-square test were used in comparisons of the foraging behavior of males and females. To insure that data were derived from independent observations, I only used information on the initial location and activity of the woodpecker for each observation period. Significance levels were scaled down using the Bonferroni procedure (Miller 1966) when multiple comparisons were made. The "experiment-wide" significance level was set at .05.

## RESULTS

### Nature of the data

Chestnut-colored Woodpeckers and Pileated Woodpeckers are represented by the fewest observations (Table 2). Both species are difficult to observe, and I did not see any Chestnut-colored Woodpeckers during most of the wet season (June–August), the same period when they are absent from lowland rain forest at Finca "La Selva," Costa Rica (Slud 1960).

I plotted saturation curves for overall niche breadth (niche breadth averaged for the six foraging variables) for both species (Fig. 1). These plots were determined by calculating overall niche breadth values for increasingly large random samples of the total observations for each species. The overall niche breadth values initially increase rapidly as the proportion of the total sample increases, but then begin to level off. This pat-

tern indicates that niche breadth values for Pileated Woodpeckers probably would not change greatly with a larger number of observations, but this is not as certain for the Chestnut-colored Woodpecker. The sample sizes are probably too small to detect subtle sexual or seasonal differences in these two species, and the niche breadth values for Chestnut-colored may be underestimated.

### Composition of the excavating guild

Only those species that excavate frequently are considered in the analysis below. The percent of time spent

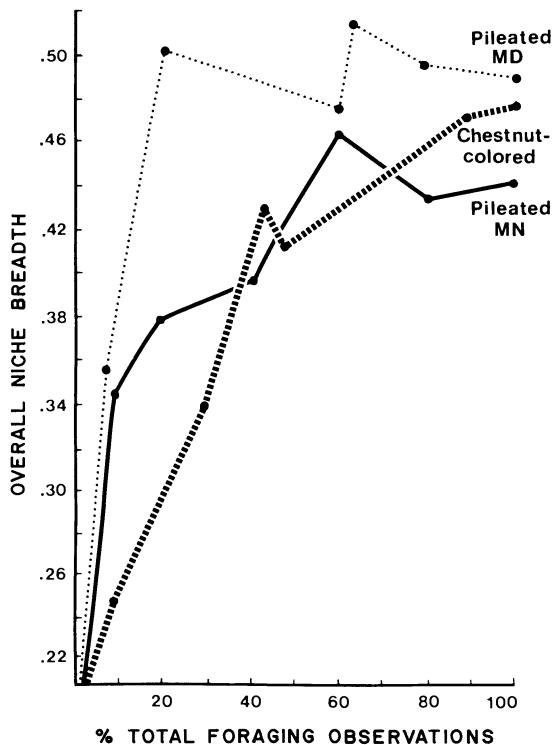


FIG. 1. Change in overall niche breadth for Pileated and Chestnut-colored woodpeckers as increasingly large proportions of the total sample size are used in the calculations. Overall niche breadth is the average of niche breadth values (Eq. 1) for six foraging variables. Values are shown for Pileated Woodpeckers at both the Minnesota (MN) and Maryland (MD) study sites.

TABLE 3. Percentage of foraging time spent on different methods of foraging for woodpecker species at three study sites.

Species	Short excavation ( $\leq 50$ s)	Long excavation ( $> 50$ s)	Probing in excavation	Probing surface	Eating fruit or nuts	Gleaning
Guatemala						
Golden-olive	38.2	16.9	15.0	24.0	0	5.8
Chestnut-colored	43.5	16.4	26.0	8.8	3.7	1.7
Lineated	27.4	32.0	29.4	11.3	0.1	0
Golden-fronted	18.6	9.5	5.7	33.8	28.1	4.3
Black-cheeked	25.2	18.2	3.6	33.0	14.1	6.1
Smoky-brown	55.5	32.7	7.2	0.6	4.1	0
Pale-billed	33.8	49.1	12.0	4.7	0	0.5
Maryland						
Pileated	18.0	55.8	6.6	8.1	11.7	0
Red-bellied	5.4	0.6	1.4	26.5	64.7	1.3
Hairy	61.9	31.8	2.9	1.8	1.7	0
Downy	59.6	16.8	2.5	9.7	11.4	0.1
Minnesota						
Pileated	3.6	82.0	12.2	1.7	0.5	0
Red-bellied	12.4	13.1	0.8	62.4	11.1	0.1
Hairy	52.2	44.6	2.3	0.8	0	0
Downy	71.5	20.7	1.2	6.1	0.4	0.1

excavating is calculated by adding the values for three foraging categories: short excavations, long excavations, and probing into excavations. Eight of the eleven species spent  $>70\%$  of their time excavating (Table 3), so they clearly must be included in the excavating guild. The Black-cheeked Woodpecker was also included because it spent nearly half of its foraging time excavating. However, Red-bellied and Golden-fronted woodpeckers spent relatively little time excavating (7–34%), and were not included in the guild.

By these criteria the excavating guild comprises six species in Guatemala and three species in Minnesota and Maryland. Thus my initial impression that the guild has nearly the same number of species in the two regions is not substantiated.

#### Seasonal comparisons

Seasonal shifts in foraging behavior are an important consideration in any analysis of resource use by different species, particularly if there is a season of scarcity when interspecific competition is accentuated (Smith et al. 1978). I therefore studied tropical woodpeckers during both the wet and dry seasons, from June to September and from January to March, respectively. I studied northern woodpeckers in both summer (16 April–14 November) and winter (15 November–15 April) in Minnesota, and early fall (9 October–14 November) and late fall and winter in Maryland. As would be expected if food sources for excavators are seasonally stable, there were relatively few seasonal differences in foraging behavior. The only significant differences at any of the study sites were for Downy Woodpeckers in Minnesota and Pileated Woodpeckers in Maryland (Askins 1981a). Both species excavated more frequently during the winter. None of

the tropical species exhibited significant seasonal differences in foraging, suggesting that even for excavators, food sources are more dependable throughout the year in a tropical rain forest. However, seasonal shifts for Downy and Pileated woodpeckers are small, and I therefore included both summer and winter data for northern species when comparing them with tropical species.

#### Sexual differences in foraging

Sexual differences in foraging behavior have been documented for many species of woodpeckers (Kilham 1965, Selander 1966, Ligon 1968). One species at each of my study sites showed such differences. In Guatemala, Lineated Woodpecker males foraged on larger branches than females ( $t = 4.83$ ,  $df = 113$ ,  $P < .001$ ). Male Downy Woodpeckers foraged on smaller branches than females in both Maryland ( $t = 5.75$ ,  $df = 164$ ,  $P < .001$ ) and Minnesota ( $t = 6.26$ ,  $df = 234$ ,  $P < .001$ ). Also, male Downy Woodpeckers excavated more than females, which spent more time probing the bark surface and eating fruit (Maryland:  $\chi^2 = 16.6$ ,  $P = .0009$ ; Minnesota:  $\chi^2 = 20.3$ ,  $P = .0001$ ). Jackson (1970) and Williams (1980) observed similar differences between the sexes of Downy Woodpeckers.

If tropical rain forest species have smaller niches than temperate forest species, then one might expect them to display greater niche overlap between the sexes (see Discussion). The amount of overlap between males and females in the use of six foraging variables was contrasted for Downy and Lineated woodpeckers to determine whether this is the case (Table 4). If all variables are considered, there is no consistent tendency for greater overlap between the sexes in the tropical Lineated than in the northern Downy. If only

TABLE 4. Niche overlap values for males and females of Lineated and Downy woodpeckers.

Species and locality	Branch diameter	Height	Wood type	Movement pattern	Foraging technique	Habitat	Average
Downy (Minnesota)	.683	.897	.980	.877	.919	.950	.884
Downy (Maryland)	.525	.862	.739	.793	.881	.942	.784
Lineated (Guatemala)	.464	.743	.852	.836	.946	.941	.797

the significantly different variables are considered, Lineated Woodpeckers show less overlap between the sexes for branch size, while Downy Woodpeckers show less overlap for foraging technique. Hence there is no clear tendency for more overlap between the sexes in the tropical than in the northern species.

#### Niche breadth comparisons

The key prediction being tested in this study is that tropical excavators do not have smaller niches than northern excavators. Therefore an average niche breadth value for all excavating species at each study site was calculated for each foraging variable. Average values for Guatemala were then plotted against those for Maryland (Fig. 2A) and Minnesota (Fig. 2B). Variables were treated separately to avoid the problems associated with combining niche breadth values for variables that are not independent (May 1975). If the values for two sites are the same, the points will lie on the diagonal. In these plots the points for nearly all of the foraging variables lie near the diagonal, indicating that niche breadths are similar for the tropical and temperate sites, as predicted by the seasonal stability hypothesis.

The point representing foraging technique is below the diagonal in both comparisons, indicating that, on average, the northern species are more specialized in their use of foraging techniques than the tropical species. This is due to the more frequent use by tropical species of techniques other than excavating, such as probing into bark crevices, gleaning, and probing into excavations (Table 3). The last technique is nearly always associated with feeding on ants and termites. Also, the tropical species eat much more fruit than Minnesota woodpeckers. They feed on the fruit of *Sabal morrisiana*, *Stemmadenia donnell-smithii*, and *Cecropia mexicana*, trees that are used by a wide variety of tropical birds, including many species that are primarily insectivorous (Eisenmann 1961, McDiarmid et al. 1977, R. A. Askins, personal observation). The availability of fruit results in tropical species having generalized foraging behavior relative to Minnesota woodpeckers. Maryland woodpeckers are more similar to those in Guatemala in this respect, since they feed on berries (see below) that are used by a wide variety of temperate-zone birds (Baird 1980).

Niche breadth values for separate foraging variables are not significantly different in comparisons of the Guatemalan species with species at each of the tem-

perate-zone sites (Mann-Whitney  $U$  Test;  $P > .05$  in all cases), with the exception of foraging technique for Minnesota (Mann-Whitney  $U$  Test;  $P < .05$ ). Also, average niche breadth values were calculated for all variables for each species, and these values do not differ significantly in comparisons of the tropical site with the northern sites (Mann-Whitney  $U$  Test;  $P >$

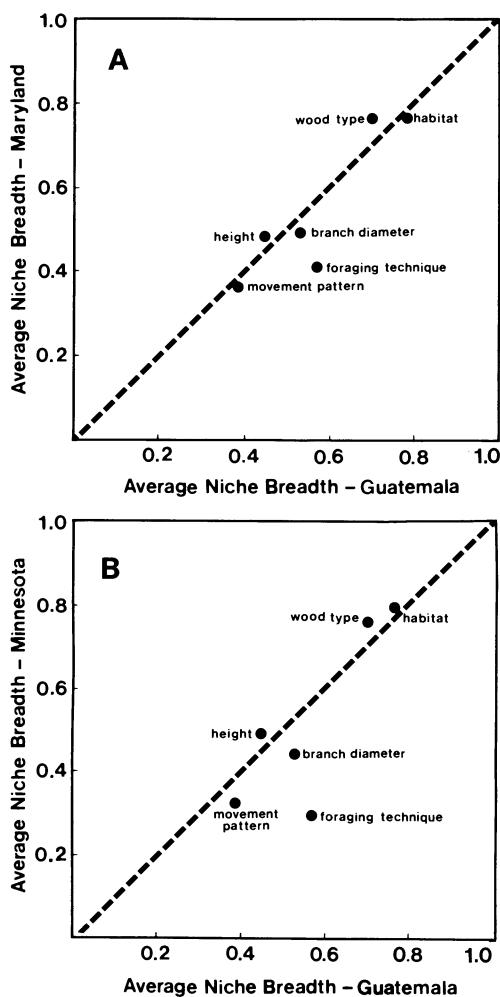


FIG. 2. Comparison of the average niche breadth values (Eq. 1) for study sites in (A) Maryland and Guatemala, and (B) Minnesota and Guatemala. These values are averages for all excavating species at a study site. The six foraging variables are shown separately. A point on the 45° dashed line would indicate equal average niche breadth values at the two study sites.

.05). Thus, tropical excavating species do not appear to have smaller niches than their temperate-zone counterparts.

Small niche breadth values of excavators in the northern habitats could be an artifact of sampling an environment with a relatively narrow range of resources. Colwell and Futuyma (1971) argue that one must compensate for the range of resources available when comparing guilds in different habitats. The use of various foraging categories by all individuals in the guild (regardless of species) gives an indication of the range of resources available at a particular locality. Niche breadth values for the entire guild are higher in Guatemala for all foraging variables except wood type, indicating that the tropical excavators use a broader range of foraging categories. To test whether this has an important effect on conclusions about relative specialization of temperate and tropical woodpeckers, I weighted the average niche breadth values for all species in the guild by the niche breadth values for all individuals in the guild in order to compensate for the greater range of resources available at some study sites. This procedure is conservative with respect to the hypothesis being tested; if the larger number of species in the tropical guild already compensates for the larger range of available resources, the weighted niche breadth values for the tropical species will be artificially low.

When the weighted niche breadth values were compared for tropical and northern species, the tropical species were more specialized for habitat and height, the northern species were more specialized for branch diameter and foraging technique, and the two groups were approximately equal with respect to wood type and movement pattern. Hence there is no consistent trend for tropical species to be more specialized.

#### Structure of the guild

The seasonal stability hypothesis correctly predicts that tropical excavators are not consistently more specialized than northern species. However, the extension of this hypothesis, that similar levels of specialization should lead to similar levels of species richness, is not supported. How can twice as many excavating species live in a tropical forest when they have niches of approximately the same size as northern species? Given the assumptions of the seasonal stability hypothesis, there are two obvious possibilities: tropical species can tolerate greater niche overlap, or there is a greater range of resources in the tropics providing more "room" for excavator niches.

The niche overlap values for separate resource variables are not significantly different for species in Guatemala and Maryland (Mann-Whitney  $U$  Test;  $P > .05$  for all comparisons). When Minnesota species are compared with Guatemalan species, however, the tropical species do appear to exhibit more overlap for branch diameter and foraging technique, and the dif-

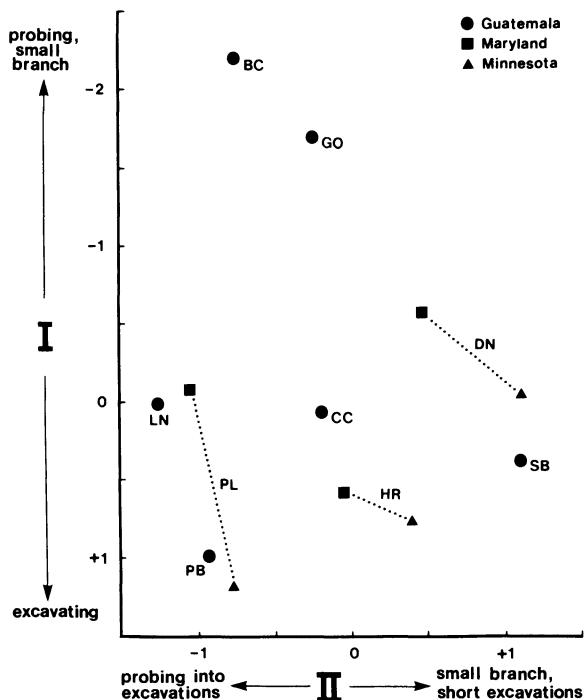


FIG. 3. Positions of woodpecker species at the three study sites with respect to the first two axes derived from discriminant analysis. The variables that made the largest contributions to each of these axes are indicated. The woodpecker species are labelled as follows: Lineated (LN), Pale-billed (PB), Pileated (PL), Black-cheeked (BC), Golden-olive (GO), Chestnut-colored (CC), Downy (DN), Hairy (HR), Smoky-brown (SB).

ference for the former is almost significant (Mann-Whitney  $U$  Test;  $.1 > P > .05$ ). These differences are largely due to small niche overlap between Pileated Woodpeckers and the other two species in Minnesota. Unlike Maryland Pileated Woodpeckers, those in Minnesota spend nearly all of their foraging time on large branches, involved in long excavations (Table 3), and this results in low average niche overlap values for the Minnesota guild. The Minnesota data support the hypothesis that tropical excavating species show greater niche overlap, thus accounting for the larger number of species in the tropical guild, but the lack of support from the Maryland data makes this explanation doubtful.

The other possibility, that excavators use a greater range of resources in the tropics, can be tested by making a graphical display of relationships among all species, both tropical and northern, in order to determine whether some of the tropical species lie outside of the ecological realm of the northern species. There are six foraging variables, however, so multivariate analysis was used to reduce the number of dimensions while minimizing the loss in information. A plot derived from discriminant analysis shows the ecological relationships among the species from all three study

TABLE 5. Description of the first two discriminant functions for an analysis of woodpecker foraging behavior at three study sites. Discriminant function coefficients with large values are underlined. The variables associated with these coefficients are used in the interpretation of the functions. Fruit eating is not included in the analysis because it had a low tolerance level.

Foraging variable	Standardized discriminant function coefficient	
	Function 1 (43.5)*	Function 2 (81.0)*
Low height	.23	.31
Small branch	<u>-.42</u>	.73
Live wood	-.10	.15
Vertical movement	.25	.15
Short excavation	<u>.59</u>	.62
Long excavation	<u>.60</u>	.29
Probe into excavation	.11	<u>-.33</u>
Probe surface	<u>-.37</u>	.23
Mature forest	.33	.32

\* Cumulative percent of variance described.

sites (Fig. 3). The first axis (I) separates species that excavate almost exclusively from those that use other foraging techniques, such as probing and fruit eating (Table 5). The second axis (II) separates species that forage on large branches and make deep excavations (large woodpeckers) from those that excavate for brief periods on small branches (small, bark-drilling woodpeckers). A plot derived from principal component analysis (PCA) has similar axes and a similar pattern of relationships among species (Askins 1981a). Also, plotting the sexes separately did not alter the basic pattern; even in species that display significant sexual differences in foraging behavior, males and females cluster close together relative to the separation among species.

Differences between Maryland and Minnesota populations of Downy and Pileated woodpeckers are as great as for many pairs of species. This is apparently due to the abundance of berries of *Rhus radicans*, *Lonicera japonica*, and *Vitis vulpina* at the Maryland site during the fall and winter, when these observations were made. At the Minnesota site Downy and Pileated woodpeckers do not have abundant berry sources even during the fall, and they spend a greater proportion of time excavating and less time eating fruit (Table 3). Consequently Maryland and Minnesota populations of these two species are separated along axis I in the discriminant analysis plot and along the probing and fruit-eating vs. excavating axis (II) in the PCA plot. Also, Dutch elm disease and windstorms killed many trees at the Minnesota site during the 4 yr of the study, and this reduced the foraging differences between the two sites. Both Downy and Hairy woodpeckers showed a significant shift in foraging during

the 4-yr period, with increased frequencies for probing and decreased frequencies for long excavations (Askins 1981a).

The most important feature of the discriminant analysis and PCA graphs is the separation of two tropical species (Golden-olive and Black-cheeked woodpeckers) from all of the temperate-zone species (Fig. 3). These two species use nonexcavating techniques such as gleaning, probing the bark surface, and fruit eating much more frequently than the other species in the guild (Table 3). Black-cheeked Woodpeckers frequently feed on fruit, and Golden-olive Woodpeckers often probe into moss and bromeliads, and tear bromeliads apart. Both species use resources not generally available to northern woodpeckers, and thus a graphical display of the guild shows these two species lying outside the "niche space" inhabited by northern species. Thus, the larger number of excavating species in the rain forest is apparently connected with a greater range of dependable resources and the greater structural complexity of the habitat.

## DISCUSSION

Comparisons of both weighted and unweighted niche breadth values for Guatemala and the two northern sites show that there is no consistent tendency for tropical woodpeckers to be more specialized than those in the temperate zone. The conclusion that northern excavators are at least as specialized as tropical excavators is also supported by a comparison of the amount of divergence in foraging behavior between the sexes in Lineated and Downy woodpeckers. Sexual differences in foraging are often found in species that have particularly large niches due to the absence of competitors (Selander 1966). Males and females appear to specialize on different "subniches" within this large niche, and this is reflected in different types of foraging by the two sexes. Sexual foraging differences would be expected in places where species have relatively large niches (such as islands and temperate-zone habitats), but not where niches are small (such as, presumably, in tropical forests). Following this line of reasoning, one would not expect the sexes of rainforest birds to differ in foraging behavior. The similar degree of sexual divergence in foraging in the tropical Lineated Woodpecker and the northern Downy Woodpecker therefore provides additional support for the contention that niche breadths are not smaller for tropical excavators.

The significance of northern woodpeckers being at least as specialized as tropical woodpeckers depends on whether this is an exceptional situation. The seasonal stability hypothesis is supported if most ecological groups exhibit greater specialization in tropical forests than in northern forests, while excavators (because of their relatively stable food supply) do not show such a difference. Actually, there are surprisingly few quantitative studies that test the common

contention that tropical birds are more highly specialized than temperate birds. My own study of Golden-fronted and Red-bellied woodpeckers, two species that were not considered members of the excavating guild, shows that the temperate-zone Red-bellied is more specialized than the tropical Golden-fronted in the use of foraging techniques, foraging heights, and branch sizes (Askins 1981a). However, several studies of northern and tropical bird guilds show that the tropical species are more specialized with respect to foraging behavior (Terborgh and Weske 1969, Stiles 1978, Rusterholz 1979) or habitat use (Howell 1971, Karr 1971, Lovejoy 1974).

Another important consideration is whether the premise of a relatively stable food supply for tropical excavators is valid. Wood-boring insects are present throughout the year even in highly seasonal environments, but their availability to woodpeckers may change seasonally, and they are only one component of the diet of wood-excavators. Pileated and Downy woodpeckers do show seasonal shifts in foraging behavior (Askins 1981a), but these changes are small compared to those reported for other temperate-zone birds (Gibb 1954, Rabenold 1980, Hutto 1981). Moreover, it is notable that all of the northern excavating species over-winter. Only female Downy Woodpeckers commonly migrate south in the winter, and they excavate less than any of the other northern excavators (Table 3). At the Minnesota study site, only 12 species of birds are permanent residents, and 4 of these are woodpeckers (3 of which are excavators). Thus woodpeckers deal with seasonal change as if they were exceptionally well buffered against it.

A relatively constant food supply does not insure stability if demand for food increases greatly during the winter as more energy is used for thermoregulation. However, woodpeckers spend most of the winter (approximately from sunset to sunrise each day) in roost cavities that provide both insulation and protection from wind. A cavity occupied by a Hairy Woodpecker was 5°–6°C warmer than the exterior of the trunk during the coldest part of two winter nights (Askins 1981b). The metabolic savings resulting from roosting in an enclosed shelter have been demonstrated for other bird species (Kendeigh 1961, White et al. 1975). Many other temperate-zone species roost in cavities, but woodpeckers have a particular advantage in being able to construct cavities of a specific shape in relatively solid wood (Short 1979).

Additional evidence that woodpeckers are buffered against seasonal changes comes, ironically, from studies in mildly seasonal tropical rain forests. Fogden (1972) found only six species of birds that molt during the dry season (a period of low insect density) in a rain forest in Sarawak. Four of these are woodpeckers, and Fogden suggests that they can molt at this time because they have a seasonally stable food supply. In high shrub habitat in Panama, Karr (1976) found

that the density and species richness of canopy birds declined markedly during the dry season. In contrast, bark-foraging birds showed relatively little seasonal change, perhaps, as Karr suggests, because they have a more dependable food supply throughout the year.

## CONCLUSION

This study provides support for the seasonal stability hypothesis, since this hypothesis correctly predicted that excavating woodpeckers (unlike other birds) would not be more specialized in the tropics than in the temperate zone. It also provides additional support for the well-established theory that more species can coexist in tropical forests because of the wider range of resources (Orians 1969, Lovejoy 1974, Pearson 1977). This appears to be the primary explanation for the greater number of excavating species in Guatemala than in the two northern localities. At least two of the three "additional" excavating species at the tropical locality appear to use a configuration of resources not used by the northern species.

However, simple explanations of patterns of species richness are unlikely to be complete (Whittaker 1972), and additional factors are probably important in determining the number of tropical woodpecker species. Tropical trees generally have smoother, thinner bark than temperate-zone trees, and this could have a direct effect on excavator diversity (Karr 1971). Also, the results of this study do not account for regional woodpecker species richness. For example, Panama has as many woodpecker species as the much larger area north of the Mexican border (American Ornithologists' Union 1957, Wetmore 1968), suggesting that on a regional scale, tropical woodpecker species have more precise habitat preferences.

## ACKNOWLEDGMENTS

This paper was submitted as part of a doctoral dissertation to the University of Minnesota Graduate School. I am grateful to the following people for their advice and criticism: my advisor, Harrison Tordoff; Edward Cushing; Patrice Morrow; Richard McGehee; Herbert Kulman; Peter Abrams; David Bruggers; Kurt Rusterholz; and Elmer Birney. John Cant, Lester Short, and Lawrence Kilham advised me in the early stages of the study and Karen Askins assisted me with the field work.

My work in Guatemala would not have been possible without the assistance and facilities provided by the Instituto de Antropología e Historia and the Parque Nacional Tikal. I am grateful to Dr. Luis Luján Muñoz, Sr. Amilcar Rene Guzmán de la Cruz, and many others for their assistance during my stay at Tikal. Also, David Correll provided me with facilities to work at the Chesapeake Bay Center for Environmental Studies, and David Torkildson gave me permission to work in Chain of Lakes Regional Park in Anoka County, Minnesota.

This research was generously funded with grants from the following sources: Minneapolis Foundation—Francis E. Andrews Fund, Smithsonian Institution, Sigma Xi (The Scientific Research Society of America), Graduate School Fellowship Office (University of Minnesota), Dayton Natural History Fund (Bell Museum of Natural History), Wilkie Fund (Bell Museum of Natural History), Department of Ecology and

Behavioral Biology (University of Minnesota), Frank M. Chapman Memorial Fund (American Museum of Natural History), and the University of Minnesota Computer Center.

#### LITERATURE CITED

- Abrams, P. A. 1980. Some comments on measuring niche overlap. *Ecology* **61**:44–49.
- Alatalo, R. H. 1978. Resource partitioning in Finnish woodpeckers. *Ornis Fennica* **55**:49–59.
- American Ornithologists' Union Committee. 1957. Checklist of North American birds. Fifth edition. Lord Baltimore Press, Baltimore, Maryland, USA.
- Andrle, R. F. 1967. Birds of Sierra de Tuxtla in Veracruz, Mexico. *Wilson Bulletin* **79**:163–187.
- Askins, R. A. 1981a. Foraging ecology of temperate-zone and tropical woodpeckers. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.
- . 1981b. Survival in winter: the importance of roost holes to resident birds. *Loon* **53**:179–184.
- Baird, J. W. 1980. The selection and use of fruit by birds in an eastern forest. *Wilson Bulletin* **92**:63–73.
- Baker, D. G., D. A. Haines, and J. H. Strub. 1967. Climate of Minnesota. Part 5. Precipitation facts, normals, and extremes. University of Minnesota Agricultural Experimental Station Technical Bulletin **254**:1–44.
- Baker, D. G., and J. H. Strub, Jr. 1965. Climate of Minnesota. Part 3. Temperature and its application. University of Minnesota Agricultural Experimental Station Technical Bulletin **248**:1–64.
- Bent, A. C. 1948. Life histories of North American nut-hatches, wrens, thrashers, and their allies. Bulletin 195, United States National Museum, Washington, D.C., USA.
- Cant, J. G. 1978. Ecology, locomotion, and social organization of spider monkeys (*Atelus geoffroyi*). Dissertation. University of California, Davis, California, USA.
- Carr, R. F., and J. E. Hazard. 1961. Map of the ruins of Tikal, El Petén, Guatemala. Tikal Report Number 11, Museum Monographs, The University Museum, University of Pennsylvania, Philadelphia, Pennsylvania, USA.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**:567–576.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1309.
- Cook, R. E. 1969. Variation in species density of North American birds. *Systematic Zoology* **18**:63–84.
- Criswell, J. H., R. Vine, R. Ford, and M. Terry. 1979. Central hardwood forest with scattered pine. *American Birds* **33**:70–71.
- Davis, J. 1973. Habitat preferences and competition of wintering juncos and Golden-crowned Sparrows. *Ecology* **54**:174–180.
- Davis, L. I., and J. Moroney. 1953. Lowland tropical forest. *Audubon Field Notes* **7**:352–353.
- Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. *Smithsonian Miscellaneous Collection* **117**:1–62.
- . 1961. Favorite foods of neotropical birds: flying insects and *Cecropia* catkins. *Auk* **78**:636–638.
- Emmons, L. H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* **50**:31–54.
- Fager, E. W. 1968. The community of invertebrates in decayed oak wood. *Journal of Animal Ecology* **37**:121–142.
- Feduccia, J. A. 1970. Natural history of the avian families Furnariidae and Dendrocolaptidae. *Journal of the Graduate Research Center, Southern Methodist University* **38**:1–26.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**:307–343.
- Gamboa, G. J., and K. M. Brown. 1976. Comparative foraging behavior of six sympatric woodpecker species. *Proceedings of the Iowa Academy of Science* **82**:179–181.
- Gibb, J. 1954. Feeding ecology of tits, with notes on Tree-creeper and Goldcrest. *Ibis* **96**:513–543.
- Graham, S. A., and F. B. Knight. 1965. Principles of forest entomology. McGraw-Hill, New York, New York, USA.
- Higman, D. 1968. An ecologically annotated checklist of the vascular flora at the Chesapeake Bay Center for Field Biology, with keys. Smithsonian Institution, Washington, D.C., USA.
- Högstedt, G. 1980. Prediction and test of the effect of interspecific competition. *Nature* **283**:64–66.
- Holdridge, L. R. 1956. A world geography of forest resources. Ronald Press, New York, New York, USA.
- Howell, T. R. 1957. Birds of a second-growth rain forest area of Nicaragua. *Condor* **59**:73–111.
- . 1971. An ecological study of the birds of the lowland pine savanna and adjacent rain forest in northeastern Nicaragua. *Living Bird* **10**:185–242.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Hutto, R. L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. *Auk* **98**:765–777.
- Jackson, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. *Ecology* **51**:318–328.
- . 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied woodpeckers in Kansas. *Condor* **78**:67–76.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* **60**:1211–1224.
- Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs* **41**:207–233.
- . 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* **110**:973–994.
- Kendeigh, S. 1961. Energy of birds conserved by roosting in cavities. *Wilson Bulletin* **73**:140–146.
- Kilham, L. 1965. Differences in feeding behavior in male and female Hairy Woodpeckers. *Wilson Bulletin* **77**:134–145.
- Klopfer, P. H. 1959. Environmental determinants of faunal diversity. *American Naturalist* **93**:337–342.
- Lawrence, L. de K. 1966. A comparative life history study of four species of woodpeckers. *Ornithological Monographs* **5**:1–156.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.
- Ligon, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. *Auk* **85**:203–215.
- Lovejoy, T. E. 1974. Bird diversity and abundance in the Amazon forest communities. *Living Bird* **13**:127–191.
- Lundell, C. L. 1937. The vegetation of Petén. Carnegie Institution of Washington, Washington, D.C., USA.
- May, R. M. 1975. Some notes on estimating the competition matrix,  $\alpha$ . *Ecology* **56**:737–741.
- McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. *Biotropica* **9**:9–25.
- Miller, R. P. 1966. Simultaneous statistical inference. McGraw-Hill, New York, New York, USA.
- Minot, E. O. 1981. Effects of interspecific competition for food in breeding Blue and Great tits. *Journal of Animal Ecology* **50**:375–385.
- Moskovits, D. 1978. Winter territorial and foraging behavior of Red-headed Woodpeckers in Florida. *Wilson Bulletin* **90**:521–535.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sci-

- ences. Second edition. McGraw-Hill, New York, New York, USA.
- Orians, G. H. 1969. The number of bird species in tropical forests. *Ecology* **50**:783-801.
- Patrick, R. 1966. The Catherwood Foundation Peruvian Amazon Expedition. Limnological studies. Monographs of the Academy of Natural Sciences of Philadelphia **14**:1-495.
- Pearson, D. L. 1977. A pantropical comparison of bird community structure on six lowland forest sites. *Condor* **79**:232-244.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**:33-46.
- Pianka, E. R., R. B. Huey, and L. R. Lawlor. 1979. Niche segregation in desert lizards. Pages 67-115 in D. J. Horn, G. R. Stairs, and R. D. Mitchell, editors. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio, USA.
- Porter, J. W. 1972. Patterns of species diversity in Caribbean reef corals. *Ecology* **53**:745-748.
- Rabenold, K. N. 1978. Foraging strategies, diversity and seasonality in bird communities of Appalachian spruce-fir forests. *Ecological Monographs* **48**:397-424.
- . 1979. A reversed latitudinal diversity gradient in avian communities of eastern deciduous forests. *American Naturalist* **114**:275-286.
- . 1980. The Black-throated Green Warbler in Panama: geographical and seasonal comparison of foraging. Pages 297-307 in A. Keast and E. S. Morton, editors. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D.C., USA.
- Recher, H. F. 1971. Bird species diversity: a review of the relation between species number and environment. *Proceedings of the Ecological Society of Australia* **6**:135-152.
- Rusterholz, K. A. 1979. Niche relations of pine foliage-gleaning birds in different competitive regimes. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. Pages 71-81 in G. M. Woodwell and H. H. Smith, editors. *Diversity and stability in ecological systems*. Brookhaven Symposia in Biology Number 22, Brookhaven National Laboratory, Upton, New York, USA.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**:408-418.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* **68**:113-151.
- Short, L. L. 1970. Notes on the habits of some Argentine and Peruvian woodpeckers (Aves, Picidae). *American Museum Novitates* **2413**:1-37.
- . 1979. Burdens of the picid hole-excavating habit. *Wilson Bulletin* **91**:16-28.
- Simpson, G. G. 1964. Species densities of North American Recent mammals. *Systematic Zoology* **13**:57-73.
- Skutch, A. F. 1969. Life histories of Central American birds. III. Pacific Coast Avifauna Number 35. Cooper Ornithological Society, Berkeley, California, USA.
- Slud, P. 1960. The birds of Finca "La Selva," Costa Rica: a tropical wet forest locality. *Bulletin of the American Museum of Natural History* **121**:49-148.
- Smith, J. N. M., P. R. Grant, B. R. Grant, I. J. Abbott, and L. K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* **59**:1137-1150.
- Smithe, F. B. 1966. The birds of Tikal. Natural History Press, New York, New York, USA.
- Stapleton, J. 1979. Maple-oak forest. *American Birds* **33**: 58.
- Stewart, R. E., J. B. Cope, C. S. Robbins, and J. W. Brainard. 1952. Seasonal distribution of bird populations at the Patuxent Research Refuge. *American Midland Naturalist* **47**:257-363.
- Stiles, E. W. 1978. Avian communities in temperate and tropical alder forests. *Condor* **80**:276-284.
- Sudd, J. H. 1967. An introduction to the behavior of ants. St. Martin's Press, New York, New York, USA.
- Tate, J., Jr. 1973. Methods and annual sequence of foraging by the sapsucker. *Auk* **90**:840-856.
- Terborgh, J. W., and J. S. Weske. 1969. Colonization of secondary habitats by Peruvian birds. *Ecology* **50**:765-782.
- Tramer, E. J. 1974. On latitudinal gradients in avian diversity. *Condor* **76**:123-130.
- Wetmore, A. 1968. The birds of the Republic of Panama. Part 2. Columbidae to Picidae. Smithsonian Institution Press, Washington, D.C., USA.
- White, F. N., G. A. Bartholomew, and T. R. Howell. 1975. The thermal significance of the nest of the Sociable Weaver *Philetairus socius*: winter observations. *Ibis* **117**:171-179.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* **21**:213-251.
- Wiens, J. 1977. On competition and variable environments. *American Scientist* **65**:590-597.
- Williams, A. B. 1947. Climax beech-maple forest with some hemlock (15 year summary). *Audubon Field Notes* **1**:205-210.
- Williams, J. B. 1980. Intersexual niche partitioning in Downy Woodpeckers. *Wilson Bulletin* **92**:439-451.
- Williams, J. B., and G. O. Batzli. 1979a. Competition among bark-foraging birds in central Illinois: experimental evidence. *Condor* **81**:122-132.
- Williams, J. B., and G. O. Batzli. 1979b. Winter diet of a bark-foraging guild of birds. *Wilson Bulletin* **91**:126-131.
- Willis, E. O. 1966. Interspecific competition and the foraging behavior of Plain-brown Woodcreepers. *Ecology* **47**: 667-672.
- Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. *Condor* **72**:169-174.