

SEASONAL CHANGES IN THE FORAGING METHODS AND HABITATS OF
SIX SYMPATRIC WOODPECKER SPECIES IN SOUTHWESTERN VIRGINIA

by

Richard Neil Conner

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APPROVED:

C. S. Adkisson, Chairman

T. A. Jenssen

R. M. Andrews

R. A. Paterson, Department Head

H. E. Burkhart

D. A. West

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Blacksburg, Virginia

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INTRODUCTION

The breadth of a species' niche and overlap between species' niches can be estimated by comparing the resources and habitats they use. Such comparisons increase our ability to understand relationships between species. However, in the past there has been controversy over the definition of "niche". A brief review of the history of the niche concept may help clarify the definition.

History of Niche Concepts

The first use of the word "niche" in an ecological sense is commonly attributed to Grinnell (1917), although Gaffney (1975) pointed out that Johnson (1910) visualized the niche as a unit of distribution affected primarily by food supply and secondarily by other environmental factors.

Grinnell (1917, 1924) developed the concept of the niche as a geographical or spatial unit. In contrast, Elton (1927) viewed the niche as "the status of a species in its community, to indicate what it is doing." Grinnell (1928) refined his concept of niche as having components of both the habitat structure where a species is found and a species' function. Vandermeer (1972) has suggested recently that Grinnell's (1928) concept of niche was the Hutchinsonian fundamental niche and Elton's (1927) concept was the Hutchinsonian realized niche.

Gause (1934) and Volterra (1926) provided insight into possible mechanisms responsible for the segregation of species' niches. Gause

developed what is now called the principle of competitive exclusion (or Principle of Gause and Volterra) which stated that two or more species could not indefinitely occupy the same niche in the same place. The idea that niche overlap indicated competition developed as a result of the concept of competitive exclusion. However, overlap does not necessarily indicate competition (Powers 1971, Weins 1976). If two or more species overlap in the utilization of a particular resource, competition would occur only if that resource were in limited supply (Crombie 1947, Weatherley 1963). Where shared resources were limited, competition could act as a selective pressure to reduce the niche overlap among species.

Hutchinson (1958) visualized the niche as a hypervolume in n -dimensional space. He considered this hypervolume as a species' "fundamental niche" when the species' entire set of physical and biological variables were included. The "realized niche", a subset of the fundamental niche, was visualized by Hutchinson as that portion of the fundamental niche in which a species actually exists because of competition with other species. Thus a species' realized niche can be viewed as an expanding and contracting hypervolume within its fundamental niche. The dynamics of the realized niche of a species result from varying degrees of competition with other species that share some aspect of the species' fundamental niche.

Some of the problems of quantifying the n -dimensional hypervolume of the realized niche were solved by Green (1971). He used a multiple discriminant analysis to analyze nine ecological parameters of 10

species of bivalve molluscs. He also discussed the value of multivariate analyses as they relate to the Hutchinsonian niche model. The reduction of a set of correlated variables to a subset of uncorrelated variables was viewed as a way to simplify and describe the axes of the niche in Hutchinson's conceptual hypervolume.

In the present study I have used the Hutchinsonian niche model and examined relationships among species using multivariate statistical techniques.

Concepts on the Response of Breadth and Overlap to Varying Food Densities

In this study terms that are used to describe the niche will refer to the foraging aspect of species' realized niches. Thus use of the terms breadth and overlap will refer only to breadth of, or overlap between, the foraging aspects of species' realized niches and not the entire niche.

In the northern temperate zone, where I conducted my study, seasonal changes might be expected to cause fluctuations in the abundance of food resources. Theoretical studies by MacArthur and Pianka (1966), Emlen (1966, 1968), MacArthur and Levins (1967), and Cody (1974) all basically predict that a species' breadth of resource use should decrease with an increase in food density, and increase with a decrease in food density. However, a field study has demonstrated the reverse. Baker and Baker (1973), in a study of shorebirds, observed narrow breadth in foraging methods and

micro-habitat used during the winter when food was presumably less dense, and wide breadth during summer when food was more abundant.

May and MacArthur (1972) have theorized that overlap should decrease when resources are limiting and increase when resources are abundant. Field studies have demonstrated this to be correct. The earliest of these showed that foraging differences in English titmice decreased (i.e. greater overlap) as the food resource became superabundant (Hartley 1953). Similar results were found when comparing several species of shorebirds (Baker and Baker 1973), male and female Hispaniolan woodpeckers (Melanerpes striatus) (Wallace 1974), and species of tropical fish (Zaret and Rand 1972). Willson (1971a) reported overlap in foraging height to be less in the spring than in the winter in 22 out of 43 pair combinations of bird species. In only six cases did overlap increase in the spring; these cases involved comparisons of downy (Picoides pubescens), red-bellied (Melanerpes carolinus), and red-headed (M. erythrocephalus) woodpeckers. Unfortunately, changes in resource availability were not mentioned for these comparisons.

Although most of these field studies found a decrease in overlap as the resource becomes less abundant, this phenomenon should not be expected to occur in all instances, but only when the demand on the resource is greater than the supply (Crombie 1947 , Weatherley 1963, Wiens 1976).

Objectives of the Project

I studied resource overlap and breadth of resource use among six woodpecker species in southwestern Virginia. There were three objectives to this study.

The first objective was to determine how six species of sympatric and often syntopic woodpeckers, the downy (Picoides pubescens), hairy (Picoides villosus), pileated (Dryocopus pileatus), red-bellied (Melanerpes carolinus), and red-headed (Melanerpes erythrocephalus) woodpeckers, and the common flicker (Colaptes auratus), differed in their use of the food resource.

A second objective was to determine if there were intraspecific differences between male and female use of the food resource in the woodpecker species where sexes could be distinguished.

My third and main objective was to determine the effect of changing resource availability on breadth and overlap of resource use for the six species of woodpeckers.

LITERATURE REVIEW

There is an abundance of literature documenting resource partitioning. Early research by Colquhoun and Morley (1943) dealt with vertical zonation in woodland bird communities. More recent studies have demonstrated resource partitioning in insectivorous birds (MacArthur 1958; Morse 1967, 1973; Hespeneide 1971; Beaver and Baldwin 1975; James 1976), shorebirds (Ashmole 1968, Holmes and Pitelka 1968), seed eating finches (Willson 1971b, Davis 1973, Allaire and Fisher 1975) and in rodents (Brown and Lieberman 1973). Orians and Horn (1969) detected resource partitioning by blackbirds but measured high overlap values in resource utilization, values that were very similar to the theoretical maximum values without excessive competition that were derived by MacArthur and Levins (1967). Rathcke (1976) also demonstrated high overlap within a guild of herbivorous insects but with minimal competition in resource use. In Rathcke's study the food resource apparently was not limiting.

Many recent studies have demonstrated directly and indirectly that morphological differences, such as bill size or body size, are highly correlated with the size of the food item taken (Schoener 1965; Hespeneide 1966, 1973, 1975; Pulliam and Enders 1971; and Diamond 1973).

Partitioning of the food resource among woodpecker species has also been observed for hairy woodpeckers and Williamson's sapsucker (Sphyrapicus thyroideus) (Stallcup 1968); downy, red-bellied and red-headed woodpeckers (Willson 1970); great spotted (Picoides

major) and northern three-toed (Picoides tridactylus) woodpeckers (Hogstad 1971); downy and hairy woodpeckers (Kisiel 1972); downy, hairy, and red-cockaded (Picoides borealis) woodpeckers (Morse 1972); red-bellied and red-headed woodpeckers (Reller 1972); downy, red-bellied, and red-headed woodpeckers, and yellow-bellied sapsuckers (Sphyrapicus varius) (Williams 1975); and red-bellied and red-headed woodpeckers (Jackson 1976).

Sexual differences in feeding, a form of intraspecific resource partitioning has been demonstrated within different species of birds and other vertebrates (Storer 1966, Schoener 1967, Morse 1968, Robins 1971, and Williamson 1971).

A number of studies have also shown sexual differences in foraging behavior in the following woodpeckers: hairy and downy woodpeckers (Kilham 1965, 1970); Hispaniolan woodpeckers (Selander 1966); Arizona (Picoides arizonae) and Strickland's (P. stricklandi) woodpeckers (Ligon 1968a, 1968b); downy woodpeckers (Jackson 1970); Megellanic (Campephilus magellanicus), Nuttall's (Picoides nuttallii), ladder-backed (P. scalaris), and hairy woodpeckers (Short 1970, 1971); downy and red-bellied woodpeckers (Willson 1970); downy and hairy woodpeckers (Kisiel 1972); red-bellied woodpeckers (Reller 1972); downy woodpeckers (Williams 1975); and northern three-toed woodpeckers (Hogstad 1976). Bock (1970), however, observed no sexual differences in the Lewis woodpecker's (Asyndesmus lewis) foraging.

The question of whether sexual differences exist in the foraging behavior of two species of woodpeckers has not been resolved yet.

Koch et al. (1970) observed vertical stratification of feeding zones during the breeding season between male and female white-headed woodpeckers (Picoides albolarvatus). Ligon (1973) also studied this species during the breeding season and failed to detect any sexual differences in feeding. Ligon (1968a) reported sexual differences in red-cockaded woodpecker foraging during the breeding season. Morse (1972), in contrast, failed to detect sexual differences in feeding in this species during the winter. This discrepancy suggests possible seasonal variation of resource use overlap by red-cockaded woodpeckers.

Austin (1976) reported seasonal variation in the foraging behavior of ladder-backed woodpeckers. When resources became limiting males tended to be generalists while females tended to specialize. Seasonal variation in food items taken by other woodpeckers and vertebrates has been well documented (Martin et al. 1951, Stefanovic 1958-59, Bent 1964, Heithaus et al. 1975, and Feinsinger 1976).

Partitioning of the nesting habitat resource has been reported for red-bellied and red-headed woodpeckers (Reller 1972 and Jackson 1976), and for downy, hairy, pileated, and red-headed woodpeckers, and common flickers (Conner 1973, Conner et al. 1975, 1977).

METHODS

Description of the Study Areas

The majority of the study area consisted of 20 km² located on the upper Craig and Poverty Creek drainages of the Blacksburg Ranger District of the Jefferson National Forest in southwestern Virginia. The two major cover types in this part of the study area were stands of oaks (Quercus spp.) and hickories (Carya spp.) which covered 60 percent of the area and stands consisting primarily of oaks and pines (Pinus spp.) which covered another 20 percent of the area. Stands of yellow-poplar (Liriodendron tulipifera), white oak (Q. alba), and northern red oak (Q. rubra), and stands of Virginia pine (P. virginiana), white pine (P. strobus), and pitch pine (P. rigida), both occupied approximately another 10 percent of the area. A wide range of cover types and successional stages, resulting from clearcutting (Conner and Adkisson 1974, 1975; Conner and Crawford 1974), were present.

The second part of the study area was centered around the town of Blacksburg and the Virginia Polytechnic Institute and State University campus. This non-forest area, although primarily in pasture, included six mature woodlots (250-350 yrs. old) of oaks and hickories. These woodlots varied between 0.5 and 20 ha. Most of the woodlots had no understory; grass was the only ground cover. Red-headed woodpeckers nested regularly in these areas (Conner 1976).

Research Design and Sampling Procedures

Foraging behavior and habitat of a woodpecker guild (for definition of guild concept see Root 1967), the downy, hairy, pileated, red-bellied, and red-headed woodpeckers, and the common flicker, were measured from September 1972 through July 1976. Data were collected during three seasons: breeding season (15 April through 15 June), post-breeding season (July through October), and Winter (December through February).

Orians and Horn (1969) have stressed the importance of measuring both food habits and habitat where foraging occurs when studying overlap of resource use between species. For this reason I recorded the foraging methods used by woodpeckers (revised from Kilham 1965) and the micro- and macro-foraging habitat where foraging occurred (Table 1). Birds were observed using 7 x 50 power binoculars. When possible, the sex of the bird was recorded. A "sample unit" for the statistical analyses comprised the behavior and habitat position of each woodpecker at the observer's initial contact with the bird. The foraging methods used by each woodpecker and their duration were also recorded until the bird disappeared from sight.

In addition to the variables listed in Table 1, I measured the following micro-habitat variables: vertical position of the woodpecker in the tree (lower, middle, and upper third), horizontal position (twig: ≤ 0.5 cm diameter, branch: ≤ 5.0 cm and > 0.5 cm, limb: > 5.0 cm, and trunk: center portion of tree from which limbs

Table 1. List of variables used in the study and the mnemonic code used for them in this paper.

Variable Code	Description of the Variable
<u>Macro-foraging Habitat</u> (3 sets of measurements at each site)	
BA	Basal Area in M ² /ha measured with a prism
DOS	Density of stems, stems > 6cm DBH, number per 1/25 ha circular plot
CH	Average height (m) to the top of the canopy crown
<u>Micro-foraging Habitat</u>	
WHGT	Height (m) of the foraging woodpecker above the ground
SDIA	Diameter of the stem of the tree (cm) where the woodpecker foraged
THGT	Height of the tree (m) that the woodpecker foraged in
TDBH	Diameter at breast height (cm) of the tree the woodpecker foraged in
<u>Foraging Methods</u>	
PP	Peer and poke, a surface gleaning technique without any disturbance to the substrate foraged on
PECK	Pecking of the foraging substrate without any subcambial penetration
SCAL	Scaling the bark off a tree in search of food items
EXCA	Sub-cambial excavation in search of food items
HAWK	Aerial forays to capture insects on the wing
VEGF	Consumption of any vegetable material
GRDF	Foraging on the ground for animal food items

project), tree quality (live, dead, dead portion of live, stump, or fallen log), and the species of tree in which foraging occurred. The additional macro-habitat variables recorded were relative age and condition of timber stand and timber type (Society of American Foresters 1954). The density of underbrush (twigs) in the zone between the ground and 3 m above the ground was subjectively estimated and placed into one of four categories ranging from least to most dense. A more precise determination of the last parameter was not possible because of the seasonal presence and absence of leaves.

The Analyses

Descriptive statistics (means, standard deviations, and ranges), one way analyses of variance, and Duncan's new multiple range test were calculated on the micro- and macro-habitat variables (Sokal and Rohlf 1969, Barr et al. 1976).

Multivariate analyses were used to extract most of the pertinent information from the data. Multivariate techniques have been used widely in studies concerning avian-habitat relationships (Cody 1968, James 1971, Whitmore 1975, Conner and Adkisson 1976, 1977). Morrison (1976) and James (1971) provide excellent descriptions of the utility and methods of principal component analysis. A major benefit of principal component analysis is that it allows the user to evaluate many species simultaneously on the same scale in hyperspace; thus it closely represents the concept of Hutchinson's (1958) realized niche.

Each species can be viewed as having a multivariate cloud of points in hyperspace.

Principal component analyses (PCA) were calculated separately on foraging methods, micro-habitat, and macro-habitat variables using an SAS program (Barr et al. 1976). Separate analyses on each subset of variables (see Table 1) were calculated in order to evaluate how the woodpecker species partitioned each aspect of the food resource (e.g. by using different macro-habitats, micro-habitats, or foraging methods). If two species foraged in totally different macro-habitats, then 100 percent overlap in micro-habitat and foraging methods would be rather meaningless since the two species would be allotopic.

Seasonal Changes in Hyperspace

Each separate PCA was calculated using the data for all species in all seasons.

Seasonal changes in each species' foraging parameters were then evaluated by selecting the observations of each species in each season from this cloud of data points. Breadth of and overlap between species' clouds of data points were then contrasted for each season. This allowed measurements of changes in similarity, breadth, and overlap between species as the seasons changed, or as the food resource availability changed.

Euclidean Distance: The Euclidean distance (in hyperspace of a PCA) between the centroids of two species was used as a measure of

similarity between species' foraging methods, micro-habitat and macro-habitat. Techniques using Euclidean distance have been used in past avian studies (Powers 1971, Conner and Adkisson 1977).

Breadth of Resource Utilization: Calculations of breadth of resource use were made using two different techniques. Breadth of foraging methods for each species was calculated using the information theory, or diversity index formula of Shannon and Weaver (1949).

Breadth of micro- and macro-habitat used was calculated by summing the variance values of each species over each component of a PCA. Levins (1968), and MacArthur and Levins (1967), have described niche, or resource breadth, as the "distance" through a niche hypervolume along a particular line in niche space. Since I am dealing with statistics rather than parameters, variance values appear to be a more accurate estimation of this "distance" than a linear measurement. I have summed the variance values along the different axes because of the multi-dimensional character of the hypervolume created by the PCA, and the fact that all the axes are orthogonal.

Overlap in Resource Utilization: Techniques measuring overlap and critiques of various techniques have been described (Horn 1966, MacArthur and Levins 1967, Colwell and Futuyma 1971, Pielou 1972, Sabath and Jones 1973). Many of these papers deal with overlap in a univariate sense (a single niche dimension), as the probability of two species encountering each other, or as competition as inferred by the overlap.

As a multivariate measurement of overlap in woodpecker foraging methods, I have summed the linear overlap of each species pair combination on each axis of a PCA over all the axes in n-dimensional space. If two species have the same repertoire of foraging methods and forage in the same micro- and macro-habitat, overlap between them can be decreased by one species' use of some methods more frequently than the other species. Thus, two species can overlap to different degrees in all foraging methods they both use. Overlap between two species for one method does not exclude the chance of overlap in other methods. Therefore, any overlap in foraging methods between species would be additive for each of the methods where overlap occurs.

In the case of micro- and macro-habitat, a different statistical technique must be used since spatial habitat variables were measured. If one woodpecker species forages primarily at the top of a tree and another at the bottom of a tree, the only overlap in physical habitat used will be that portion where the birds overlap somewhere in the middle of the tree. If both these species fed only on 1 cm diameter branches (i.e. complete overlap), actual overlap of spatial habitat would still only be the amount that their vertical distributions in the tree were shared. Minimal overlap, as recently noted by Harner and Whitmore (In press), can be calculated between two multivariate observations by a two-group discriminant function analysis (Fisher 1936, 1938, Freeze 1964, Dixon 1974). Multivariate normality for both groups is an assumption for this technique (Harner and Whitmore, In press).

I have calculated discriminant analyses for each species pair combination with all seasons included, and then separated out each season to measure the overlap (now reduced to overlap on a single line) as it changes for each season. These measurements revealed the changes in overlap of physical habitat used by woodpeckers as the food resource varied. It should be noted that these overlap measurements are not synonymous with competition, or the probability of one species encountering another.

Assumptions on Food Resource Availability

Measurement of woodpecker food resource availability was not feasible. As a substitute I made assumptions as to when the food resource would be abundant and when it would be scarce. Since woodpeckers are omnivores and consume both insects and vegetable material (Beal 1911, Martin et al. 1951), they will be dependent on the seasonal availability of these food items. Insects will be most abundant during late spring, summer, and fall, but relatively scarce, at least on the surface of trees, during winter. The vegetable matter that woodpeckers eat consists mainly of fruits and seeds (acorns) which are abundant in late summer and fall, but become scarce in winter and spring. Based on this information, I have assumed that woodpecker food will be moderately available during the breeding season, abundant in the post-breeding season, and scarce in the winter.

RESULTS AND DISCUSSION

A fairly complete set of information on foraging behavior was collected on all species except the red-bellied woodpecker (Table 2). Data are adequate for this species to contrast its macro-habitat with that of the other five species. Since common flickers foraged primarily on the ground and red-headed woodpeckers mainly caught insects in the air or fed on acorns they had wedged in tree limbs, micro-habitat variables (Table 1) were analyzed statistically only for the downy, hairy, and pileated woodpeckers.

Comparisons Among Species

Macro-Habitat

Partitioning of macro-habitat by the six species of woodpeckers was examined several ways. Forest timber types (Society of American Foresters, 1954) were used to evaluate habitat selection on a basis of tree species composition (Table 3). The oak-hickory forest type was used most often by all of the woodpecker species except the common flicker which used park-like habitat such as open campus areas most often. The downy and hairy woodpeckers showed the most diverse selection of timber types, while the red-headed woodpecker showed the least diversity (Table 3). Downy and pileated woodpeckers were found in habitats with pines (18 and 17 percent, respectively), and hairy woodpeckers (11 percent).

Table 2. Sample sizes and mnemonic codes for woodpecker species.

(BR- breeding season, P-BR- post-breeding season, W- winter)

Species	Macro-habitat			Micro-habitat			Foraging Methods		
	BR	P-BR	W	BR	P-BR	W	BR	P-BR	W
Downy (D)	123	195	150	39	64	50	32	60	47
Hairy (H)	105	177	129	33	57	43	30	52	39
Pileated (P)	117	114	117	35	36	39	29	31	56
Flicker (CF)	117	84	69	39	28	23	39	27	23
Red-bellied (RB)	12	45	21	2	14	5	2	12	4
Red-headed (RH)	57	63	99	19	21	33	19	21	33
D males	54	87	66	17	28	22	13	25	21
D females	69	108	84	22	36	28	19	35	26
H males	48	81	66	15	27	22	14	25	20
H females	57	96	63	18	30	21	16	27	19

Table 3. Percentages of timber types used by different woodpeckers with corresponding H' values (Shannon and Weaver 1949).

Timber type	: D	: H	: P	: CF	: RB	: RH
Oak-Hickory	53	62	72	5	76	96
Pitch pine-Oak	7	5	9	4	2	
Yellow poplar- Red & White oak	8	10	7		4	
Open Campus	8			71	18	2
Suburb-low brush open	3	2		6		
Chestnut oak	9	10	4			
White pine-Oak	8	3	4	1		
Scarlet oak	1	5				
Fields				13		2
Pitch pine	1		4			
Hemlock-Hardwood	1	3				
Table Mt. pine	1					
Diversity Index (H')	1.68	1.35	1.01	1.05	0.72	0.20

The woodpeckers were also evaluated on a basis of age or condition of the habitat selected. All species except the common flicker were found mostly in mature stands of timber (Table 4). The flicker used lawns, young clearcuts, and edge habitat; these are areas with adequate access to the ground for foraging. The red-headed woodpeckers were found in mature timber 87 percent of the time (Table 4). In all cases the habitats used by this species were campus woodlots that were park-like and devoid of an understory. Grasses and forbs were the only ground cover in the woodlots.

The red-headed woodpecker's and flicker's use of areas with an open understory was best observed with a subjective estimate of density of vegetation within 3 m of the ground (Fig. 1). The downy, hairy, and pileated woodpeckers used habitat with denser vegetation near the ground. Red-bellied woodpeckers foraged in areas with the most dense understory vegetation (Fig. 1).

A better view of similarities and differences between woodpecker use of macro-habitat is given by measurements of basal area, density of stems, and canopy height. Although overlap is present among all woodpecker species for all three variables (Fig. 2), there are significant differences ($P < 0.05$) between species (Table 5). It is interesting to note that pileated woodpeckers used stands with the highest average basal area and density of stems. Conner et al. (1975) observed a similar phenomenon in pileated woodpecker selection of nesting habitat. Red-headed woodpeckers used habitat with the highest mean canopy height, a high basal area, and a low density of

Table 4. Percentages of timber classes used by different woodpeckers.

Timber Class	: D	: H	: P	: CF	: RB	: RH
Non-stocked Clearcut	3		2	27	4	2
2-6 yr old Clearcut <i>(see 3)</i>	2	1		29		
6-12 yr old Clearcut <i>SP</i>	3	5	5	10	12	
Pole stand Timber	22	23	18		4	
Mature Saw Timber	66	70	72	14	72	87
Edge of Mature Timber	4	1	2	20	8	11

Figure 1. Density of vegetation between the ground and 3 m up in areas where woodpeckers foraged. (See Table 2 for species code.)

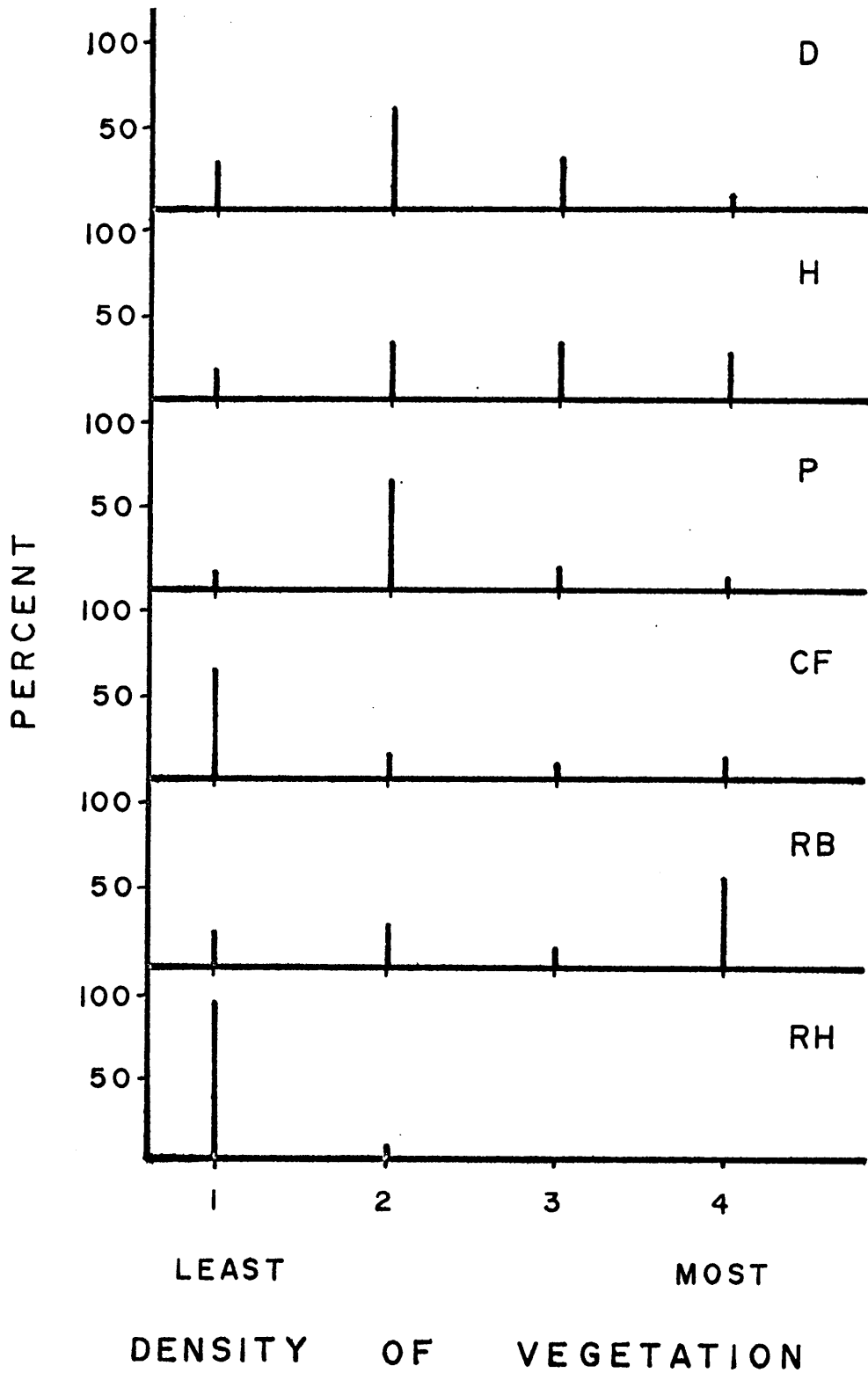


Figure 2. Range, standard deviation, and means for macro-habitat variables at woodpecker foraging sites. (See Tables 1 and 2 for mnemonic variable and species codes.)

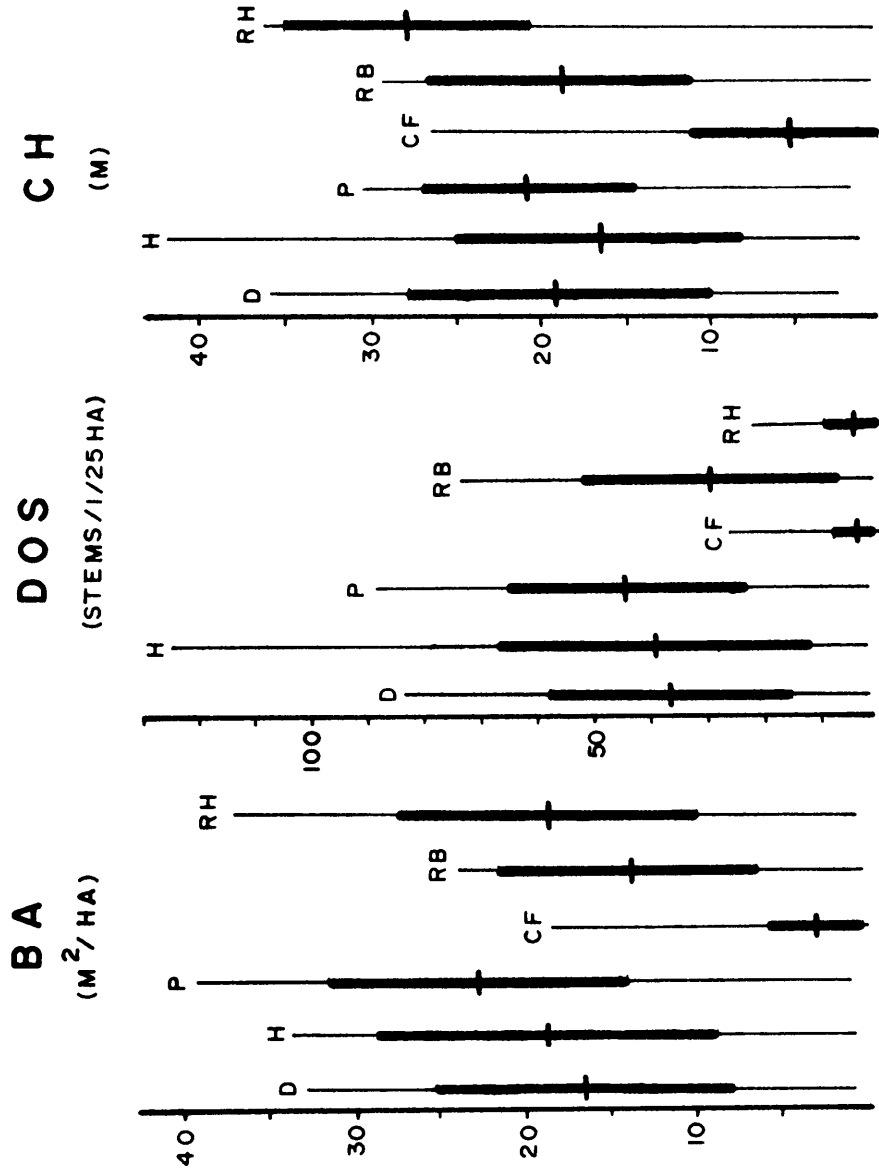


Table 5. Duncan's New multiple range test of macro-foraging habitat data. Common line indicates non-significant differences, $P < 0.05$.

Variable	: Species order in descending means					
Basal Area (m ² /ha)	P	RH	H	D	RB	CF
	<u>22.7</u>	<u>19.8</u>	<u>18.5</u>	<u>16.5</u>	14.2	<u>2.6</u>
Density of Stems (no. of stems > 6cm DBH/ 1/25 ha)	P	H	D	RB	RH	CF
	<u>43.8</u>	<u>39.5</u>	<u>36.8</u>	<u>30.0</u>	<u>5.8</u>	<u>3.1</u>
Canopy Height (m)	RH	P	RB	D	H	CF
	<u>28.4</u>	<u>21.0</u>	<u>19.0</u>	<u>18.5</u>	16.7	<u>5.9</u>

stems (Fig. 2), confirming their preference for an old mature forest. The common flicker's use of relatively open, unvegetated areas was seen in its selection of areas with the lowest average basal area, density of stems, and canopy height (Fig. 2). Downy, hairy, and red-bellied woodpeckers consistently used habitat intermediate to the other woodpecker species (Fig. 2). In contrast to the observations of Anderson and Shugart (1974), downy woodpeckers used habitats with a higher average canopy height than did hairy woodpeckers.

A principal component analysis (Table 6) and a correlation matrix (Table 7) were calculated on the three macro-habitat variables. Basal area, as would be expected, was highly correlated with canopy height. Correlations of the components to the original variables show that canopy height and basal area (also correlated to the third component) are highly correlated to the first component (positive correlations), while density of stems is highly correlated (negative correlation) to the second component (Table 6). The first two components explain more than 93 percent of the total variation (Table 6).

A plot of each species' distribution on the first two components demonstrates a high degree of overlap in macro-foraging habitat selection (Fig. 3). Common flickers and red-headed woodpeckers' use of habitats with a low density of stems is readily seen. The flicker, however, also used areas of low basal area and canopy height (Fig. 3).

The results thus far have demonstrated considerable partitioning of an aspect of the food resource for some of the species. Common

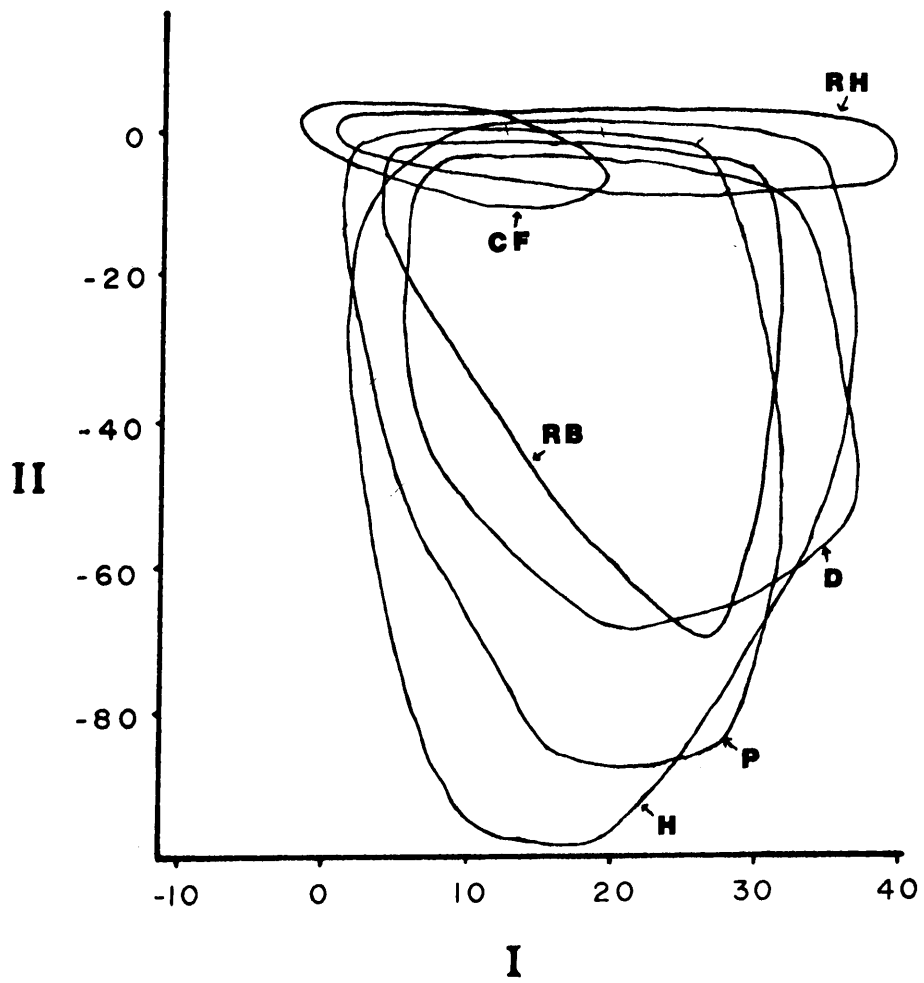
Table 6. Results of the principal component analysis of the macro-foraging habitat variables for all six species of woodpeckers. (See Table 1 for mnemonic variable codes.)

	Component		
	I	II	III
Percentage of total variance accounted for	66.8	26.5	6.7
Cumulative percentage of total variance accounted for	66.8	93.3	100.0
Correlations of components to original variables			
BA	0.44	-0.33	-0.84
DOS	0.07	-0.97	-0.23
CH	0.94	-0.07	-0.32

Table 7. Correlation matrix of macro-foraging habitat variables for the principal component analysis on all six species of woodpeckers. (See Table 1 for mnemonic variable codes.)

	BA	DOS
DOS	0.55	
CH	0.70	0.21

Figure 3. Woodpecker species macro-habitat plotted on the first two principal component axes. A circle is drawn around the individual observations for each species. The first component from left to right represents increasing canopy height and basal area. The second component from low to high represents decreasing densities of stems. (See Table 2 for species code.)

Macro- Habitat

flickers and red-headed woodpeckers selected macro-habitats greatly different from those selected by the other four species.

Micro-Habitat

A comparison of micro-habitat among species revealed additional differences. There were differences in the species of trees used by woodpeckers (Table 8). Hairy, red-headed, and pileated woodpeckers selected oaks more than 60 percent of the time, while downy woodpeckers selected oaks less than 50 percent. Conifers were used by pileated and downy woodpeckers (19 and 12 percent respectively) more than by hairy woodpeckers (4 percent) (Table 8). Kisiel (1972) also observed that hairy woodpeckers used conifers less than downy woodpeckers.

Common flickers spent most of their time on the ground (76 percent). When foraging in trees, they selected dogwoods (Cornus florida) most often (11 percent). Dogwoods were used by flickers mostly in the post-breeding season when they ate the fruits.

Downy woodpeckers foraged on hickories more than any other species (Table 8). This may have been because of the pattern of the bark which provides many places for insects to hide. Downy woodpeckers used superficial foraging methods more than any of the other woodpecker species; these methods are well suited to exploit the foraging substrate available on hickories. Downy woodpeckers have been shown to prefer certain species of trees in other geographical areas, also apparently because of their use of superficial foraging techniques

Table 8. Percentages of tree species used by foraging woodpeckers with corresponding H' values (Shannon and Weaver 1949).

Species of tree	D	H	P	CF	RH
<u>Quercus prinus</u>	11	22	26	6	
<u>Q. rubra</u>	11	10	19	3	23
<u>Q. coccinea</u>		8	6		
<u>Q. alba</u>	25	28	10		41
<u>Q. velutina</u>	1				
<u>Carya spp.</u>	16	10	7		8
<u>Acer rubrum</u>	4		4		
<u>Pinus rigida</u>	2	2	13		
<u>P. strobus</u>		2	6		
<u>P. pungens</u>	9				
<u>Liriodendron</u>					
<u>tulipifera</u>	2	3	1		
<u>Magnolia acuminata</u>			4		
<u>Cornus florida</u>	4	1		11	3
<u>Platanus occidentalis</u>		4			
<u>Gaultheria procumbens</u>				3	
<u>Betula niger</u>	2				
<u>Rhus spp.</u>	1	1	1	1	
<u>Vitis spp.</u>	1		1		
<u>Oxydendrum arboreum</u>		1			

Table 8 (cont.). Percentages of tree species used by
foraging woodpeckers.

Species of tree	D	H	P	CF	RH
<u>Prunus serotina</u>	3	5	1		
<u>Robinia pseudoacacia</u>		1			3
<u>Ulmus americana</u>	1				
<u>Tsuga canadensis</u>	1				
<u>Salix babylonica</u>	2	1			
<u>Nyssa sylvatica</u>	3				
<u>Juglans nigra</u>					6
Other (ground, air)	1	1	1	76	16
Diversity index (H')	2.4	2.2	2.1	0.8	1.5

(Kilham 1961, 1970). Downy woodpeckers demonstrated the most diverse selection of tree species and common flickers the least (Table 8).

There were differences in the conditions of the trees used by different species of woodpeckers (Table 9). Pileated woodpeckers foraged mostly on dead wood (62 percent); in Oregon they showed a similar trend (Bull 1975). Downy and hairy woodpeckers foraged mostly on live wood (70 and 56 percent, respectively) which agrees closely with what Kisiel (1972) observed in New York. When not foraging on the ground, flickers foraged about the same amount of time in dead trees as in live (Table 9). Red-headed woodpeckers foraged mainly in live trees.

There were differences in the vertical positions used by foraging woodpeckers. Positions selected by downy and hairy woodpeckers were quite similar, while pileated woodpeckers used mainly the lower third of trees (Table 10). Common flickers, when in trees, foraged mainly on fruits in the top third of the trees. Red-headed woodpeckers foraged mostly in the upper two thirds of mature oaks; acorns were most abundant there.

There were differences in use of horizontal positions. Downy woodpeckers foraged mainly on trunks and branches, while hairy woodpeckers concentrated more on limbs (Table 11). Pileated woodpeckers foraged mainly on trunks (88 percent) (Table 11). When foraging in trees, red-headed woodpeckers typically spent some time out on twigs collecting acorns (7 percent), but most time was spent eating them or storing the acorns on limbs and trunks (Table 11).

Table 9. Condition of the trees selected by different species of foraging woodpeckers (percentages).

Substrate	D	H	P	CF	RH
Live tree	70	56	36	14	53
Dead tree	4	14	49	10	6
Dead part of live tree	22	26	9	1	24
Stump			3		
Fallen log	1	2	1	5	
Not on tree	3	2	2	70	16

Table 10. Vertical positions of foraging woodpeckers
(percentages).

Vertical position	D	H	P	CF	RH
On the ground	0	0	2	79	9
Lower third of tree	21	12	58	2	13
Middle third of tree	51	53	30	2	25
Upper third of tree	25	33	10	17	46
In the air	3	2	0	0	7

Table 11. Percentages of horizontal positions in trees selected by different woodpecker species.

Horizontal position	D	H	P	CF	RH
Trunk	40	31	88	10	22
Limb	18	40	6	0	43
Branch	30	25	2	0	13
Twig	9	1	1	14	7
Not in tree	3	2	2	76	16

Acorn storing by red-headed woodpeckers has been observed by others (Kilham 1958, MacRoberts 1975).

The downy, hairy, and pileated woodpeckers were the only species examined for the micro-habitat variables (Table 1). Each of the three species foraged at significantly different heights from each other (Table 12, Fig. 4). Pileated woodpeckers foraged at the lowest average height on the largest average diameter stems in trees that had the lowest average height and diameter at breast height (DBH) (Fig. 4). Hairy woodpeckers foraged in taller trees than did downy woodpeckers (Fig. 4, Table 12). This may account for the fact that they foraged at greater heights than downy woodpeckers since height of the tree foraged in was highly correlated with height of the woodpecker in the tree (Table 13).

A principal component analysis was calculated on the data for micro-habitat variables (Table 1) for the downy, hairy, and pileated woodpeckers (Table 14). The first two components explain almost 90 percent of the total variance (Table 14). Distributions of the three species were plotted on these two axes (Fig. 5). The first component is negatively correlated with tree height, height of the woodpecker, and DBH of the tree (Table 14). The second component is highly correlated (positive) with diameter of the stem foraged on. Although there are no areas of non-overlap among the three species, a rather extensive area of overlap of all three species is readily detectable (Fig. 5). Extensive overlap in macro-habitat was also observed for these three species (Fig. 3).

Table 12. Duncan's new multiple range test of micro-foraging habitat data. Common line indicates non-significant differences, $P < 0.05$.

Variable	Species order in descending means		
	H	D	P
Woodpecker Height (m)	<u>11.3</u>	<u>8.8</u>	<u>5.4</u>
	P	H	D
Diameter of Stem (cm)	<u>26.5</u>	<u>12.2</u>	<u>11.9</u>
	H	D	P
Tree Height (m)	<u>18.1</u>	<u>15.4</u>	<u>14.7</u>
	D	H	P
Tree DBH (cm)	<u>40.5</u>	<u>40.0</u>	<u>35.1</u>

Figure 4. Range, standard deviation, and means for micro-habitat variables at woodpecker foraging sites. (See Tables 1 and 2 for mnemonic variable and species codes.)

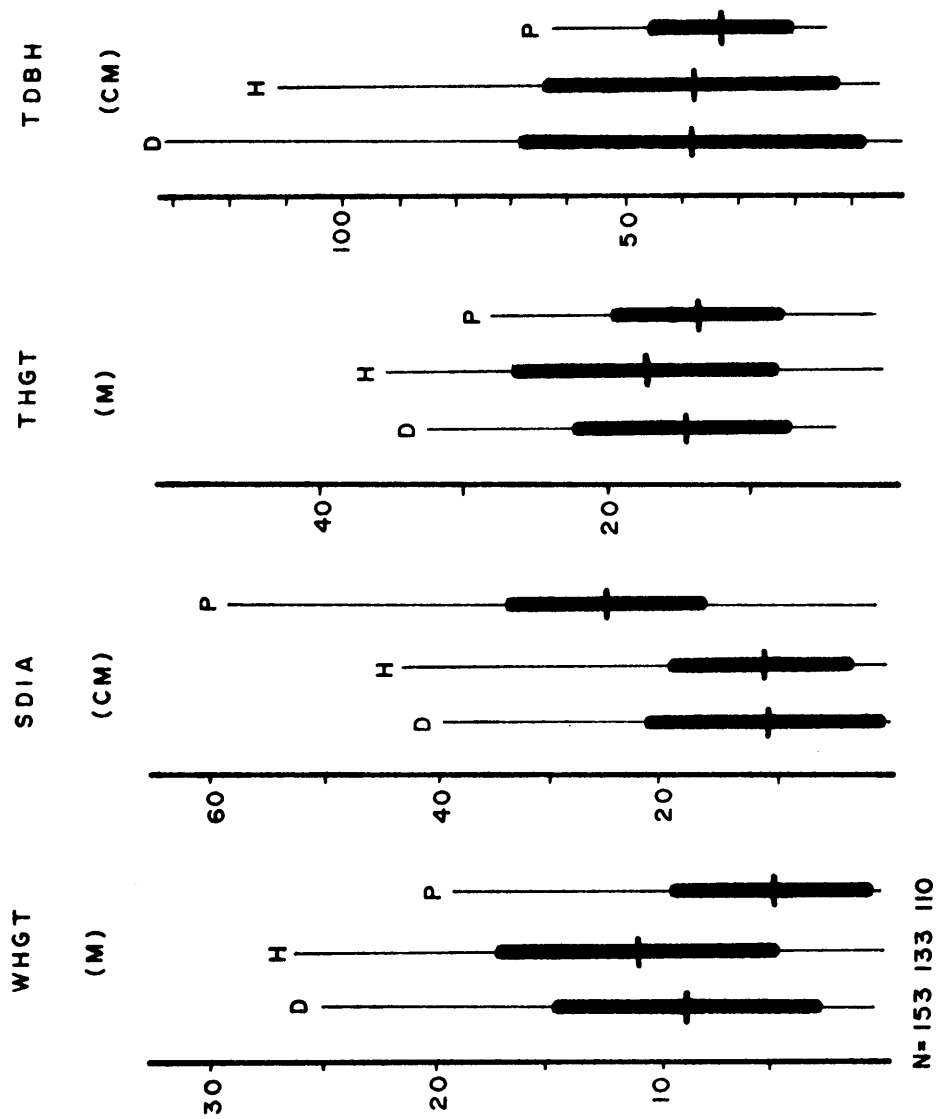


Table 13. Correlation matrix of micro-foraging habitat variables for the principal component analysis on the downy, hairy, and pileated woodpeckers (See Table 1 for mnemonic variable codes).

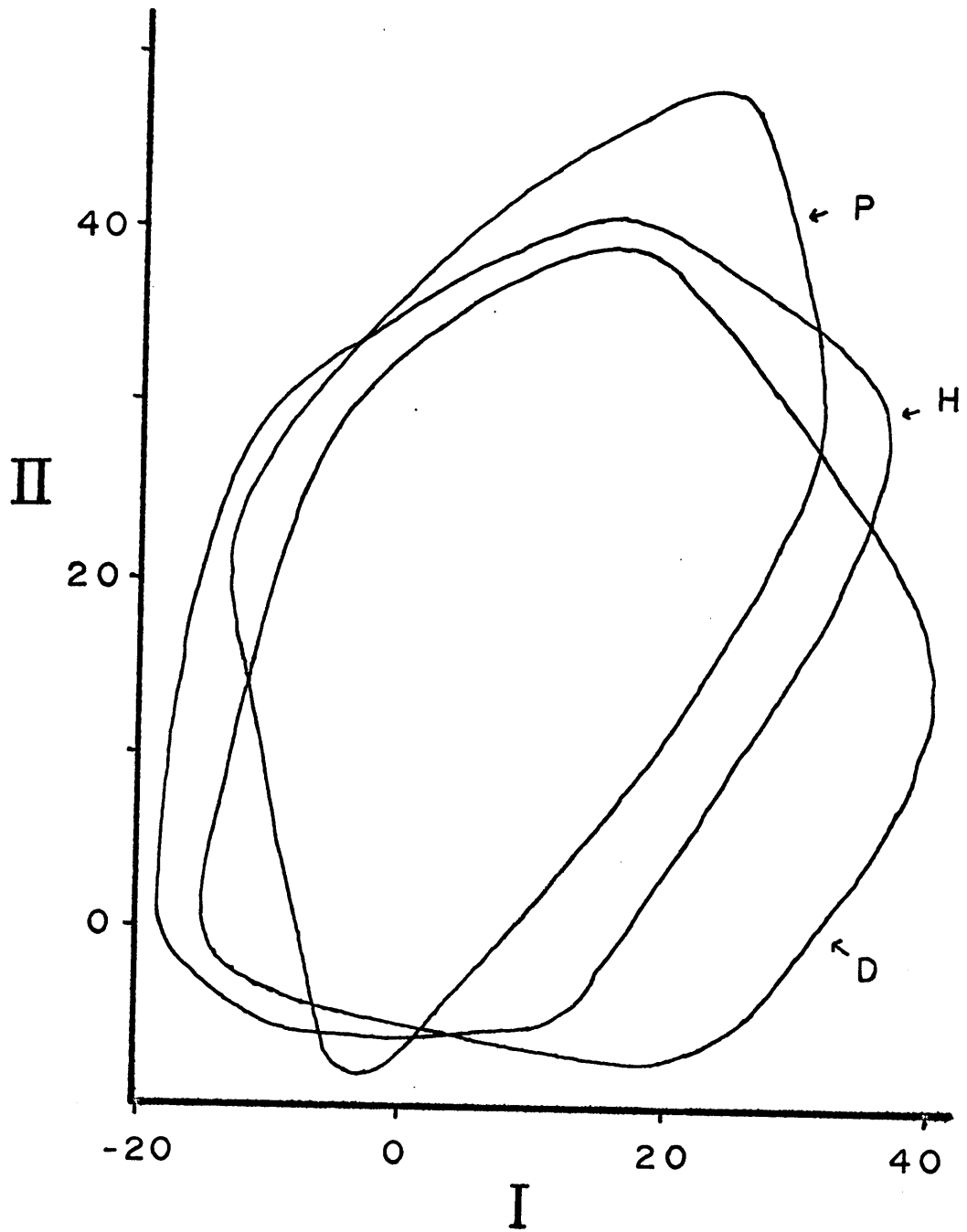
	WHGT	SDIA	THGT
SDIA	-0.22		
THGT	0.76	0.13	
TDBH	0.65	0.12	0.76

Table 14. Results of the principal component analysis of the micro-foraging habitat variables for the downy, hairy, and pileated woodpeckers. (See Table 1 for mnemonic variable codes.)

	Component			
	I	II	III	IV
Percentage of total variance accounted for	61.3	27.5	7.3	3.9
Cumulative percentage of total variance accounted for	61.3	88.8	96.1	100.0
Correlations of components to original variables				
WHGT	-0.34	-0.17	0.33	0.86
SDIA	-0.06	0.99	0.06	-0.10
THGT	-0.79	0.11	0.42	0.43
TDBH	-0.31	0.08	0.90	0.30

Figure 5. Woodpecker species micro-habitat plotted on the first two principal component axes. A circle is drawn around the individual observations for each species. The first component from left to right represents decreasing height and DBH of the tree foraged on, and height of the woodpecker above the ground. The second component from low to high represents increasing diameters of the stems foraged on. (See Table 2 for species code.)

MICRO - HABITAT

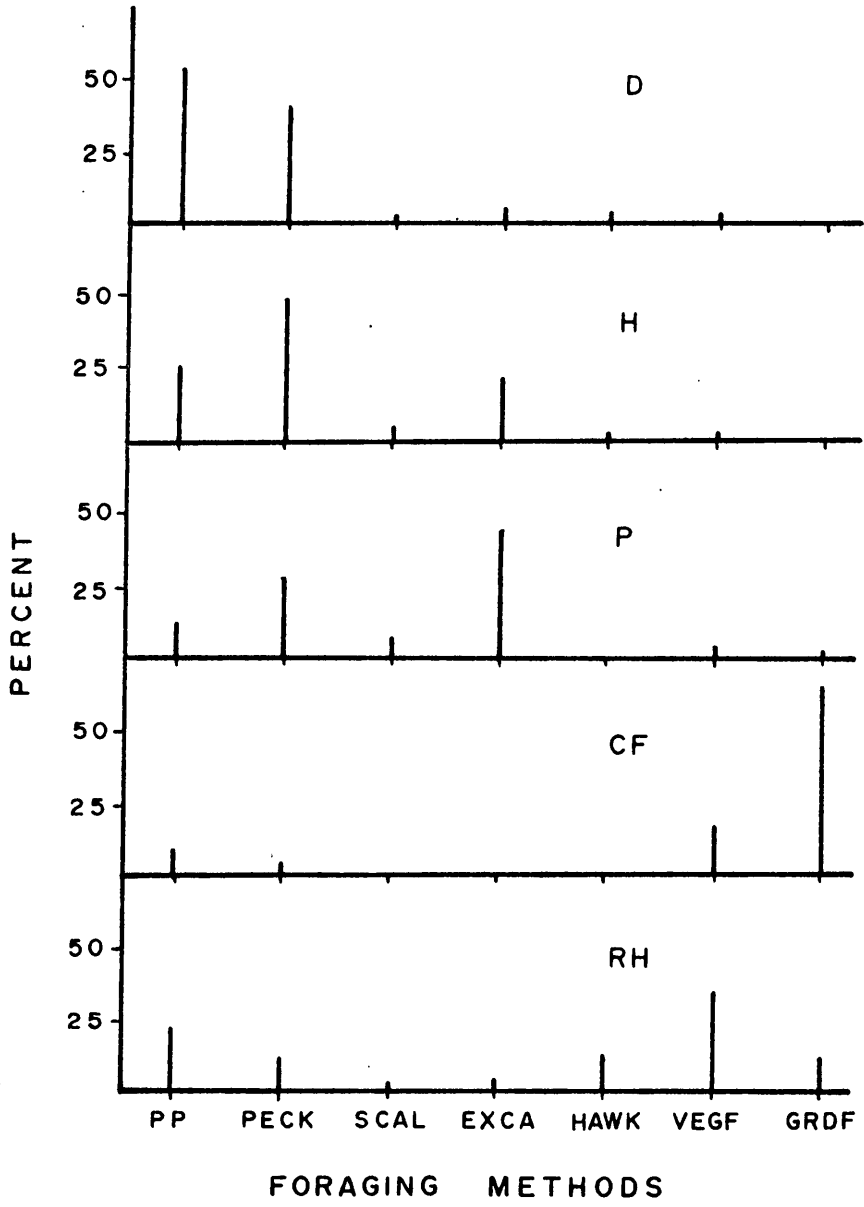


Foraging Methods and Food Items

A third way that food resources can be partitioned among woodpeckers is for different species to use different foraging methods. Because of bill structure and bill size, certain species are better able to exploit particular food resources than others (Schoener 1965). An excellent example of this is the gradation seen in bill size and foraging methods used when comparing downy, hairy, and pileated woodpeckers. The downy woodpecker has the shortest and least massive bill (mean length of 18.0 mm, Massachusetts specimens, Schoener 1965), and used mostly superficial foraging methods; the peck and poke method was used more than 50 percent of the time (Fig. 6). Hairy woodpeckers have a longer more massive bill (mean length of 31.0 mm, Massachusetts specimens, Schoener 1965) than downy woodpeckers and pecked and excavated more often than their smaller congener (Fig. 6). Pileated woodpeckers, having the longest and most massive bill (mean length upper culmen 55.6 mm, n = 11, northeastern U.S. specimens measured by the author at Virginia Polytechnic Institute and State University), excavated almost 50 percent of the time and pecked more than 30 percent (Fig. 6). The pileated woodpecker also fed more extensively on vegetable matter than did the downy and hairy. Although there were differences in foraging methods used by these three species considerable overlap was still present.

Although not quantified, my observations suggest that downy, hairy, and pileated woodpeckers also overlapped in the food items

Figure 6. Percentages of foraging methods used by different species of woodpeckers (See Tables 1 and 2 for variable and species codes.)



eaten. I observed that all three species extracted and ate beetle larvae (unidentified), termites (Isoptera), and carpenter ants (Camponotus spp.). In the winter, carpenter ants were the pileated woodpeckers' most important food item. The woodpecker typically excavated a series of deep (5-8 cm), elongated (6-15 cm) trenches into both live and dead trees in pursuit of pupae and adults. Using rapid darting movements of their tongue, pileated woodpeckers ably extracted their prey, as Kilham (1976) and Hoyt (1950) also described. Hoyt (1957) noted that carpenter ants were the pileated woodpecker's chief food item during the winter in New York, as did Conway (1957) in Missouri. Although hairy woodpeckers occasionally excavated into carpenter ant galleries, they and downy woodpeckers obtained most of the ants they ate from the surface of trees or from recent foraging excavations of pileated woodpeckers (Conner, In press).

Downy, hairy, and pileated woodpeckers were all seen eating poison ivy (Rhus spp.) berries, dogwood fruits, and grapes (Vitis spp.) during the post-breeding season. Pileated woodpeckers also appeared to eat tulip poplar (Liriodendron tulipifera) flowers that had fallen on the ground. Since there were ants on the flowers, the flower pieces may have been consumed unintentionally. Pileated woodpeckers frequently fed on the fruits of cucumber trees (Magnolia acuminata). They would hang upside down on twigs of the tree in order to peck and eat the fruits. This foraging method was also observed by Kilham (1976) when he observed them eat fruits of camphor trees (Cinnamom camphora) in Georgia.

Bill size and body size have been shown to be highly correlated with prey or food item size (Schoener 1965, Hespeneide 1966, Diamond 1973). However, the bill sizes of downy, hairy, and pileated woodpeckers may not be related as much to size of prey as to the extent that the woodpeckers penetrate trees when foraging. My casual observations of food item sizes selected by the three species as well as observations by others (Beal 1911, Martin et al. 1951) indicate that they select food items of similar sizes. I have observed that carpenter ant galleries typically lie in the center of trees of substantial size (12 cm + DBH). Pileated woodpeckers are able to feed regularly on carpenter ants because they have a large enough bill and body to make the extensive excavations (even through living oak) necessary to feed on this resource. Downy woodpeckers have the smallest bill and body size and are thus limited in their ability to penetrate when excavating for food. The hairy woodpecker falls in between the downy and pileated woodpeckers in bill and body size, and in the capability to penetrate into trees when foraging.

Common flickers and red-headed woodpeckers used foraging methods quite different from the other three species (Fig. 6). Flickers spent almost 70 percent of their foraging time on the ground. While bare ground or grass less than 15 cm high were frequented most often, they also foraged in grass up to 1 m high in fields and dense deciduous growth up to 1.5 m high in clearcuts. Ants were the major prey item, with beetles (Coleoptera), arachnids, and orthopterans also taken. When probing ant chambers flickers used two methods. They would peck but

would also pry up the ground using their bill as a lever. In the post-breeding season flickers foraged extensively on dogwood fruits, wintergreen berries (Gaultheria procumbens), and poison ivy berries.

Red-headed woodpeckers used a diverse range of foraging methods (Fig. 6). Acorns were eaten most often, especially in the post-breeding and winter seasons. They were stored in crevices and small holes in tree trunks, limbs, and branches during the post-breeding season and early winter. These stores were used in late winter and early spring as a food source. Dogwood fruits were also taken regularly during the post-breeding season and winter.

The results of a principal component analysis on foraging methods of the downy, hairy, pileated, and red-headed woodpeckers, and common flicker did not explain enough variation in the first two components (only 35 percent) to warrant plotting species distributions (Table 15). This lack of a substantial proportion of the total variation being accounted for by a small number of components was because there were few substantial correlations among the foraging methods variables (Table 16).

Sexual Differences in Foraging Behavior

Insufficient data were collected on pileated and red-bellied woodpeckers to contrast differences between males and females. Only the downy and hairy woodpeckers and the common flicker will be examined.

Table 15. Results of the principal component analysis of the foraging methods variables for the downy, hairy, pileated, and red-headed woodpeckers, and the common flicker. (See Table 1 for mnemonic variable codes.)

	Component			
	I	II	III	VI
Percentage of total variance accounted for	18.0	17.1	14.8	14.6
Cumulative percentage of total variance accounted for	18.0	35.1	49.9	64.5
Correlations of components to original variables				
PP	-0.94	-0.22	-0.14	-0.19
PECK	0.16	-0.13	0.91	-0.31
SCAL	0.09	0.46	0.09	-0.06
EXCA	0.18	0.83	-0.17	-0.03
HAWK	0.01	-0.06	-0.13	0.34
VEGF	0.10	-0.14	0.03	0.90
GRDF	0.56	-0.42	-0.60	-0.34

Table 16. Correlation matrix of foraging methods variables for the principal component analysis on the downy, hairy, pileated, and red-headed woodpeckers, and common flicker. (See Table 1 for mnemonic variable codes.)

	PP	PECK	SCAL	EXCA	HAWK	VEGF
PECK	-0.21					
SCAL	-0.12	-0.04				
EXCA	-0.30	-0.19	0.08			
HAWK	-0.09	-0.12	-0.06	-0.07		
VEGF	-0.24	-0.25	-0.11	-0.19	0.01	
GRDF	-0.29	-0.30	-0.14	-0.21	-0.04	-0.16

Downy and Hairy Woodpeckers

Because of their similarity in behavior and taxonomic classification, the downy and hairy woodpeckers will be discussed together. I was unable to detect any significant differences in macro-habitat between sexes of either species. There were, however, differences in micro-habitat.

Male downy woodpeckers foraged mainly in the middle and upper third of trees, while females used the middle and lower third (Table 17). Hairy woodpeckers showed an opposite response as males foraged mainly in the middle third and females in the middle and upper third of trees (Table 17).

Male downy woodpeckers foraged on branches and twigs while females used trunks and limbs most often (Table 18). This agrees closely with what Jackson (1970) and Kisiel (1972) observed. Male hairy woodpeckers used trunks and limbs to forage on while females selected limbs and branches more often (Table 18).

Female downy and male hairy woodpeckers have the greatest difference in bill size if both sexes of both species are compared (for bill and body size differences see Willson et al. 1975). They also overlapped more in use of horizontal foraging positions (Table 18) than any other pair combination of the four groups. The extreme difference in bill size may allow this overlap.

Male and female downy woodpeckers showed very little difference in use of live and dead trees as foraging sites (Table 19). Jackson (1970), however, has demonstrated that differences do exist when

Table 17. Percentages of vertical positions used by foraging male and female downy and hairy woodpeckers.

Vertical Position	Male Downy	Female Downy	Male Hairy	Female Hairy
Lower third of the tree	7	29	12	9
Middle third of the tree	49	56	73	41
Upper third of the tree	44	16	15	50

Table 18. Percentages of horizontal positions used by male and female downy and hairy woodpeckers.

Horizontal Position	Male Downy	Female Downy	Male Hairy	Female Hairy
Trunk	14	59	50	21
Limb	7	26	34	45
Branch	52	13	14	34
Twig	26	2	2	0

Table 19. Percentages of substrate used by male and female downy and hairy woodpeckers.

Substrate	Male Downy	Female Downy	Male Hairy	Female Hairy
Live	70	73	61	53
Dead	5	5	20	12
Dead section of live tree	25	22	19	34

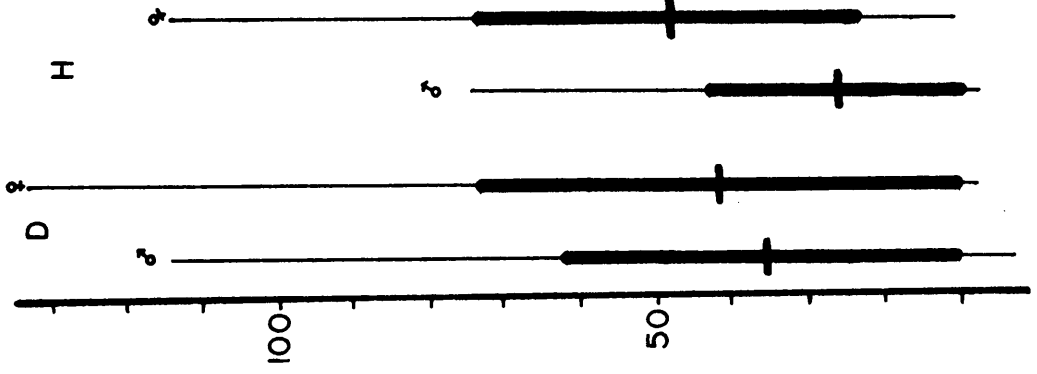
height of the woodpecker is considered simultaneously. In contrast, male and female hairy woodpeckers foraged on different quality substrates (Table 19). Both sexes selected live trees most often, but males used dead snags more than females, and females selected dead sections of live trees more than males. Female hairy woodpeckers in New York selected live trees to a greater extent than males (Kisiel 1972). This was not the case in my study (Table 19).

There were some significant differences (ANOVA, $P < 0.01$ in micro-habitat variables between male and female downy woodpeckers. Male and female downy woodpeckers foraged on significantly different mean stem sizes (3.6 and 15.6 cm, respectively), and significantly different height trees (12.4 and 16.8 m, respectively) (Fig. 7). I detected no difference between sexes in height of the woodpecker from the ground as did Jackson (1970), whose observations were made primarily in mature forest areas. Male downy woodpeckers foraged on small diameter stems; in mature forests these stems would be located high above the ground. My study included clearcuts and other areas of low second growth, where male downy woodpeckers could find small diameter stems closer to the ground than in Jackson's study. Thus, it appears that male downy woodpeckers cue more on diameter of stem than on height in the tree.

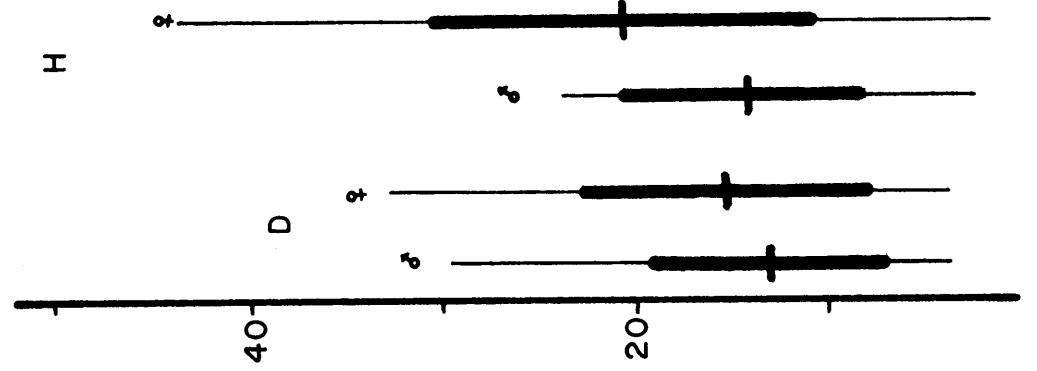
Male and female woodpeckers were significantly different (ANOVA, $P < 0.01$) in all micro-habitat variables (Fig. 7) except diameter of stem foraged on.

Figure 7. Range, standard deviation, and means for micro-habitat variables at foraging sites of male and female downy and hairy woodpeckers. (See Tables 1 and 2 for mnemonic variable and species codes.)

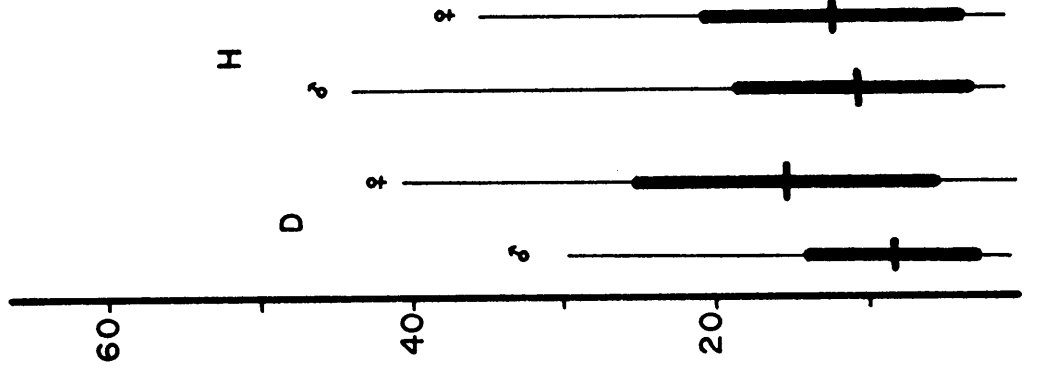
TDBH
(CM)



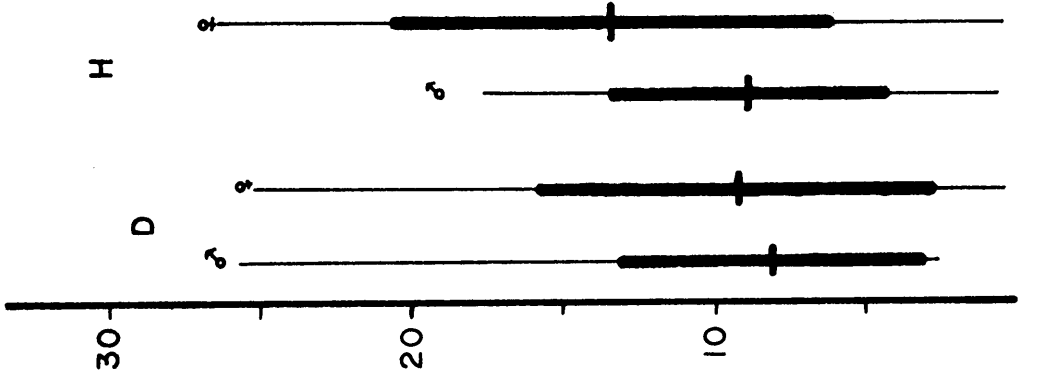
THGT
(M)



SDIA
(CM)



WHGT
(M)



Since downy and hairy woodpeckers are congeners, similarities in foraging behaviors of the two might be expected. It is interesting to note that mean values for all the micro-habitat variables for female downy and hairy woodpeckers are greater than those for their respective males (Fig. 7).

Male and female downy woodpeckers demonstrated some differences in foraging methods (Fig. 8). Females used the peer and poke method mainly on trunks and limbs. Males pecked mainly on branches and twigs (Fig. 8).

There were only slight differences in foraging methods between male and female hairy woodpeckers (Fig. 9).

Common Flickers

I detected no significant or important subjective differences between male and female common flickers in all aspects of foraging behavior.

Annual Variation in Foraging Habitat

The downy and hairy woodpeckers were the only two species out of the six examined that showed any significant differences (ANOVA, $P < 0.05$) in macro-habitat variables (basal area, density of stems, and canopy height) between years. Since these two woodpeckers have been shown in the past to concentrate on areas of high food abundance (Blackford 1955, Yeager 1955, Koplín 1969), their shift in

Figure 8. Percentages of foraging methods used by male and female downy woodpeckers. (See Table 1 for mnemonic variable code.)

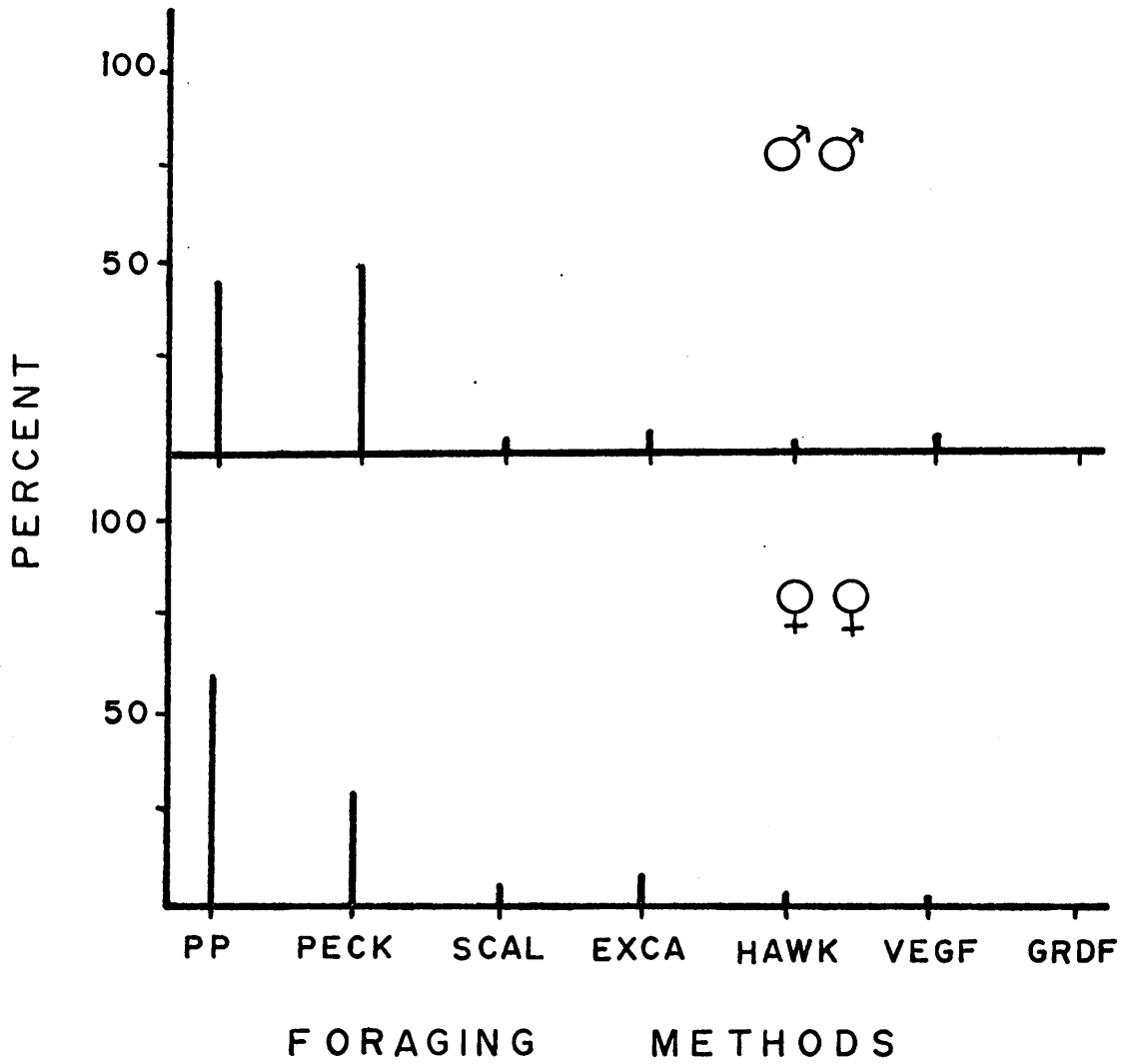
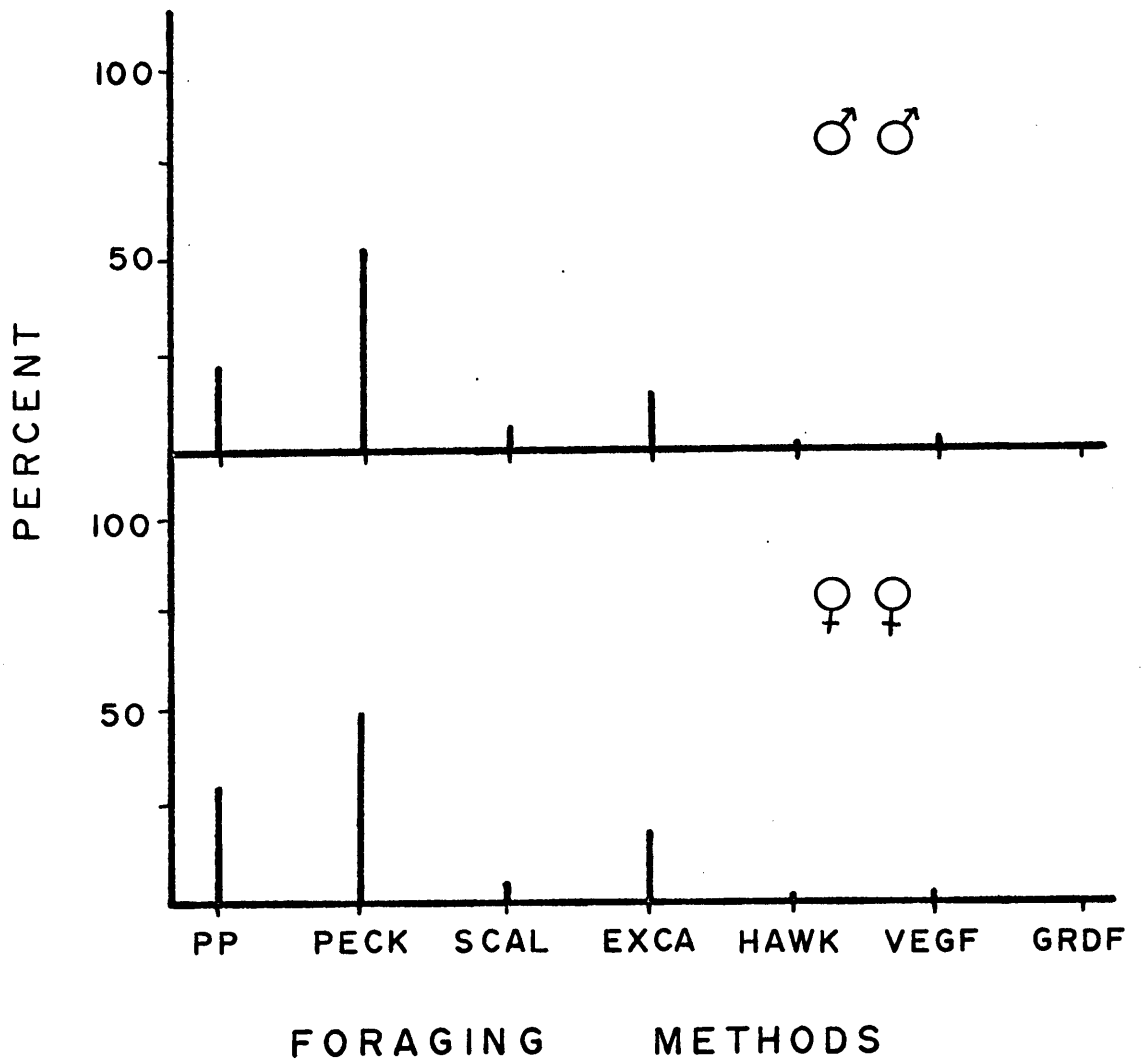


Figure 9. Percentages of foraging methods used by male and female hairy woodpeckers. (See Table 1 for mnemonic variable code.)



macro-habitat might be explained as shifts to exploit concentrations of prey.

Seasonal Variation in Foraging Methods

Woodpeckers responded to seasonal changes in food types and locations of food items by varying foraging methods used to obtain food. Downy, hairy, and pileated woodpeckers demonstrated similar changes in foraging methods between the post-breeding season and winter. They used foraging methods that penetrated deeper in the tree (Figs. 10, 11, 12). This change appears to be a response to the location of insect prey. During the post-breeding season when insects are readily available on the surfaces of trees, peer and poke, and pecking methods were used most often. In the winter when ants and insect pupae are under the bark or inside the cambium and other insects are not abundant on the surface of trees, the woodpeckers excavated more in search of prey (Figs. 10, 11, 12). Jackson (1970) also noticed that downy woodpeckers used subsurface methods more in the winter.

Seasonal changes in foraging methods of common flickers included mainly an increase in the percent of time spent eating vegetable material in the post-breeding season (Fig. 13). Red-headed woodpeckers hawked for insects and foraged on the ground most in the breeding season (Fig. 14). During the post-breeding and winter seasons these two methods were used less as red-headed woodpeckers began to eat and store acorns (Fig. 14).

Figure 10. Percentages of foraging methods used by the downy woodpecker during the breeding, post-breeding, and winter seasons. (See Table 1 for mnemonic variable code.)

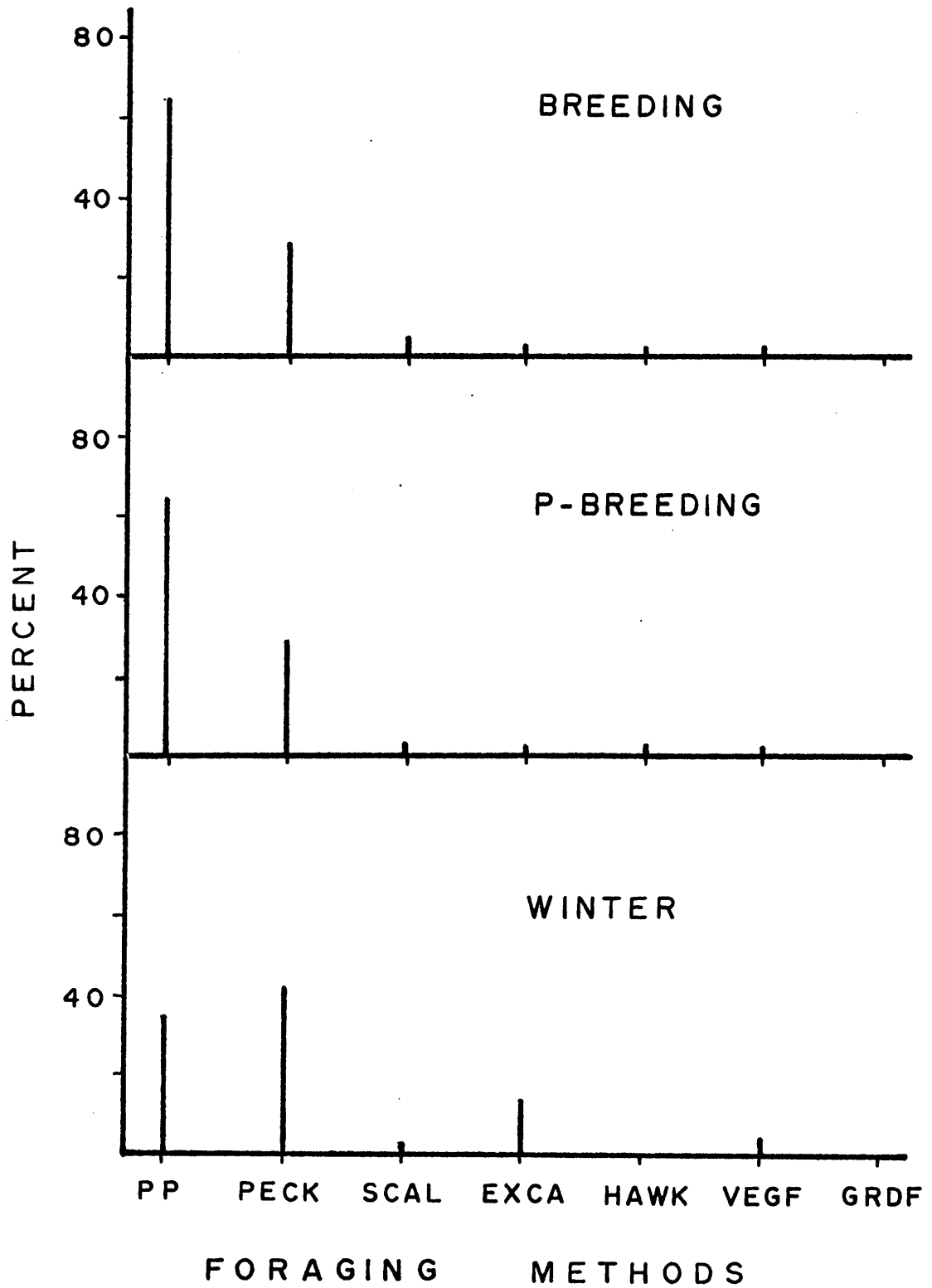


Figure 11. Percentages of foraging methods used by the hairy woodpecker during the breeding, post-breeding, and winter seasons. (See Table 1 for mnemonic variable code.)

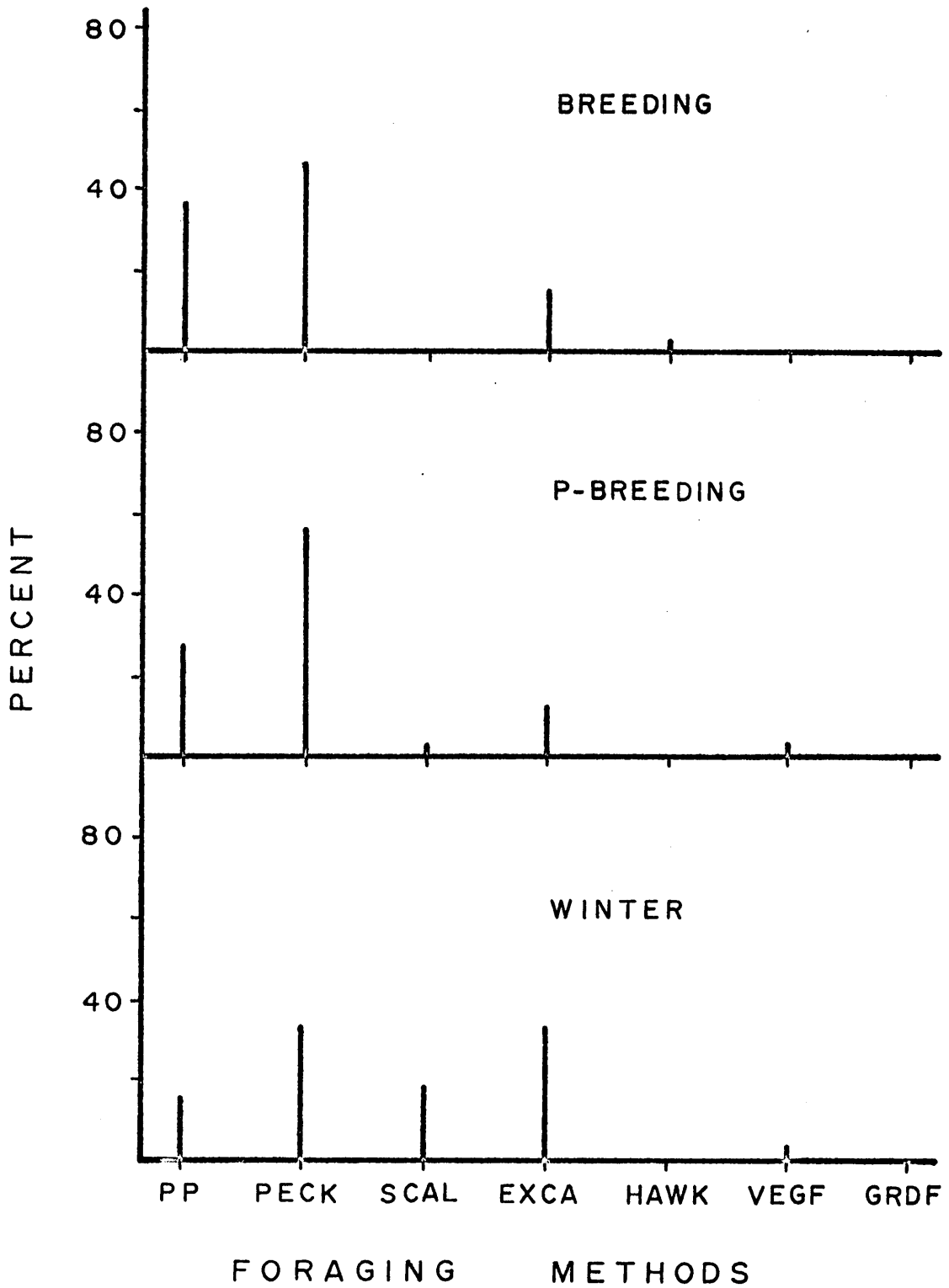


Figure 12. Percentages of foraging methods used by the pileated woodpecker during the breeding, post-breeding, and winter seasons. (See Table 1 for mnemonic variable code.)

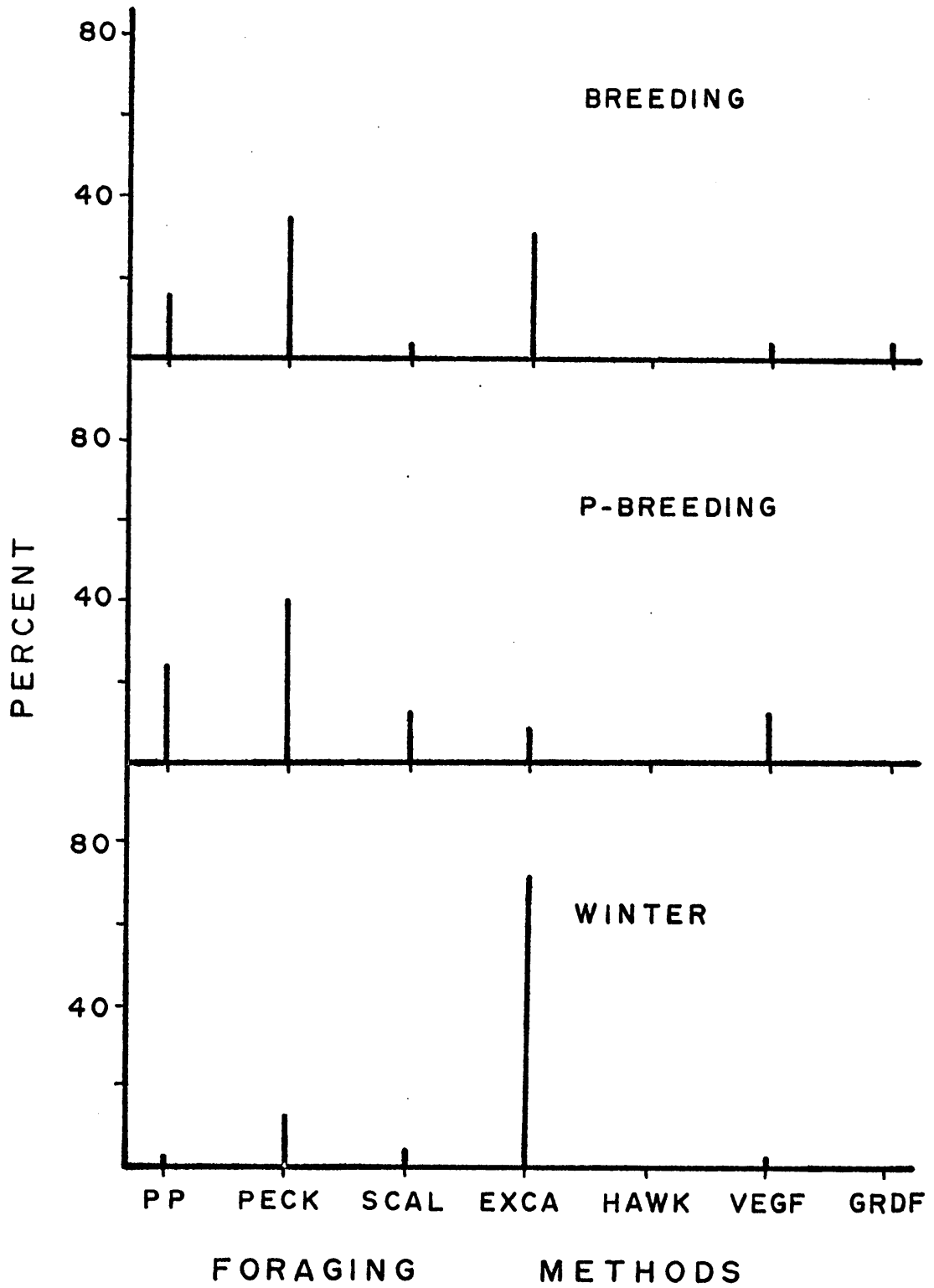


Figure 13. Percentages of foraging methods used by the common flicker during the breeding, post-breeding, and winter seasons. (See Table 1 for mnemonic variable codes.)

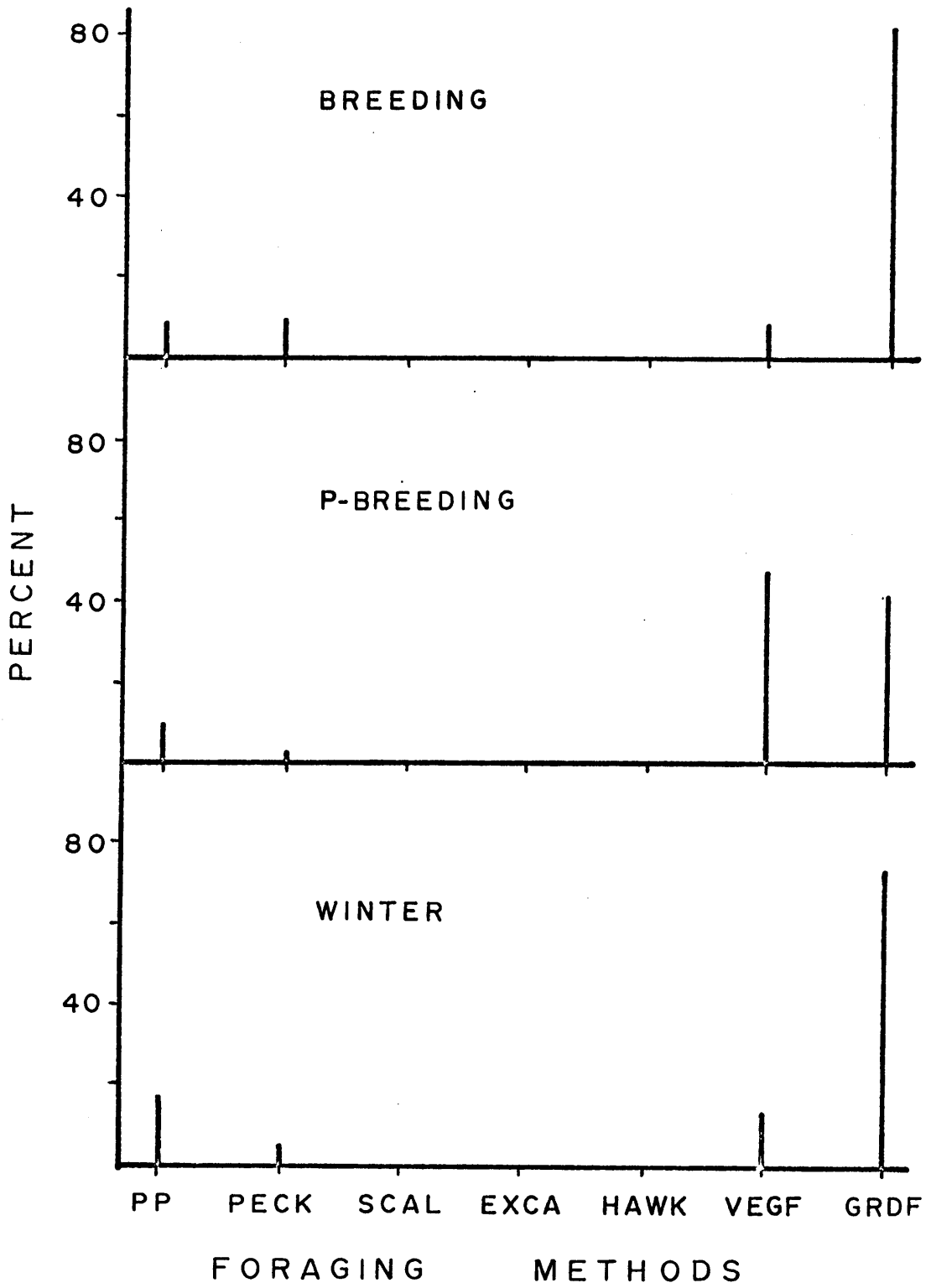


Figure 14. Percentages of foraging methods used by the red-headed woodpecker during the breeding, post-breeding, and winter seasons. (See Table 1 for mnemonic variable codes.)

Seasonal Changes in Similarity, Breadth, and Overlap

Breadth as a Function of Resource Availability

A complete view of foraging breadth can only be obtained by examining all important aspects of a species' food resource. This is because changes in macro- and micro-habitat, and foraging methods can occur independently; collectively, they reflect the breadth of food resource use.

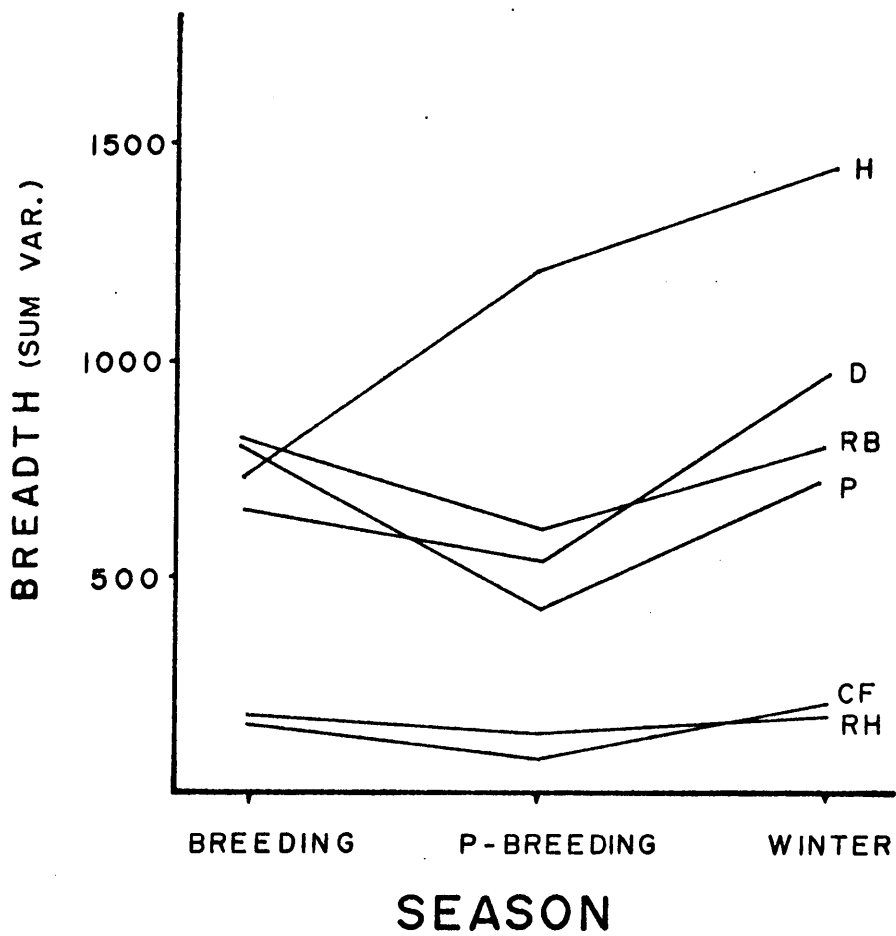
Theoretical models predict that breadth of resource use should decrease as food density increases, and increase as food density decreases (MacArthur and Pianka 1966, Emlen 1966, 1968, MacArthur and Levins 1967). Breadth of macro-habitat use was examined for all six species using a principal component analysis. Through all seasons common flickers and red-headed woodpeckers were very specific (narrow breadth) in their use of macro-habitat when compared to the other four species (Fig. 15).

As resource availability changed, five of the six species responded as would be expected based on predictions (Fig. 15). Breadth was relatively high in the breeding season (food moderately available, decreased in the post-breeding season (food abundant), and increased during winter (food relatively scarce). The hairy woodpecker was the only species to deviate from this pattern, showing an increase in breadth of macro-habitat use between the breeding and post-breeding seasons (Fig. 15).

Changes in breadth of macro-habitat used are probably best viewed when compared between the two extremes of resource availability,

Figure 15. Breadth of the macro-habitats used by six species of woodpeckers during the breeding, post-breeding, and winter seasons. (See Table 2 for species code.)

MACRO- HABITAT



post-breeding and winter seasons. From this point of view, a favorable behavior pattern is to increase the breadth of macro-habitat used (Fig. 15). Species would either increase the size of the area they foraged in or exploit additional types of habitats (basal area, density of stems, and canopy height) within their existing home range that they had not used during the post-breeding season.

When micro-habitat is examined, changes in breadth are quite variable (Fig. 16). Pileated woodpeckers selected a narrower range of micro-habitat in the winter than in the post-breeding season, opposite of what was predicted. This reflects their frequent excavations into tree trunks in the winter to gain access to carpenter ant galleries. Hairy woodpeckers responded completely opposite to what was predicted, with narrow breadth in the breeding season, wide in the post-breeding season, and narrow again in the winter (Fig. 16). Downy woodpeckers exhibited a near perfect response to what was predicted in their changes in breadth (Fig. 16).

Downy woodpeckers also exhibited the predicted responses in their changes in breadth of foraging methods (Fig. 17), but were the only species to do so. Pileated and red-headed woodpeckers and common flickers showed a decrease in breadth of foraging methods between the post-breeding season and winter; downy and hairy woodpeckers demonstrated an increase (Fig. 17).

Differences between species in changes in breadth of micro-habitat and foraging methods from the post-breeding season to winter probably reflect utilization of different types of prey by the

Figure 16. Breadth of the micro-habitats used by three species of woodpeckers during the breeding, post-breeding, and winter seasons. (See Table 2 for species code.)

MICRO- HABITAT

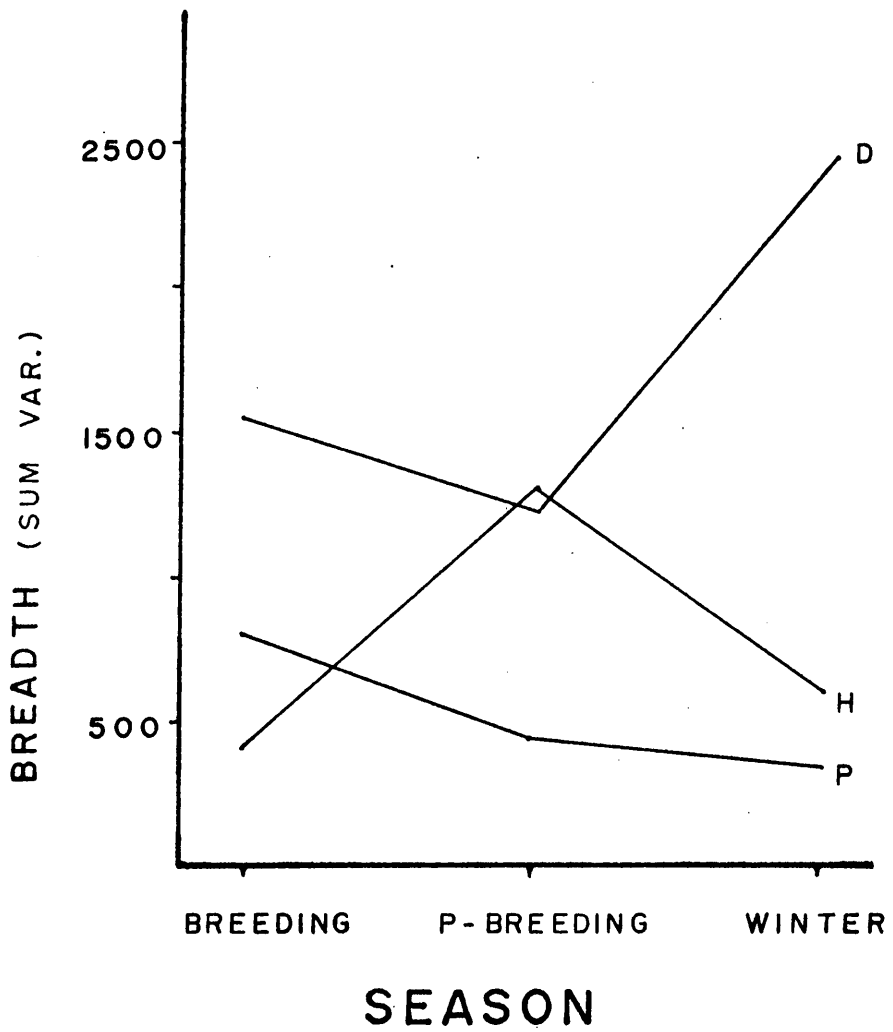
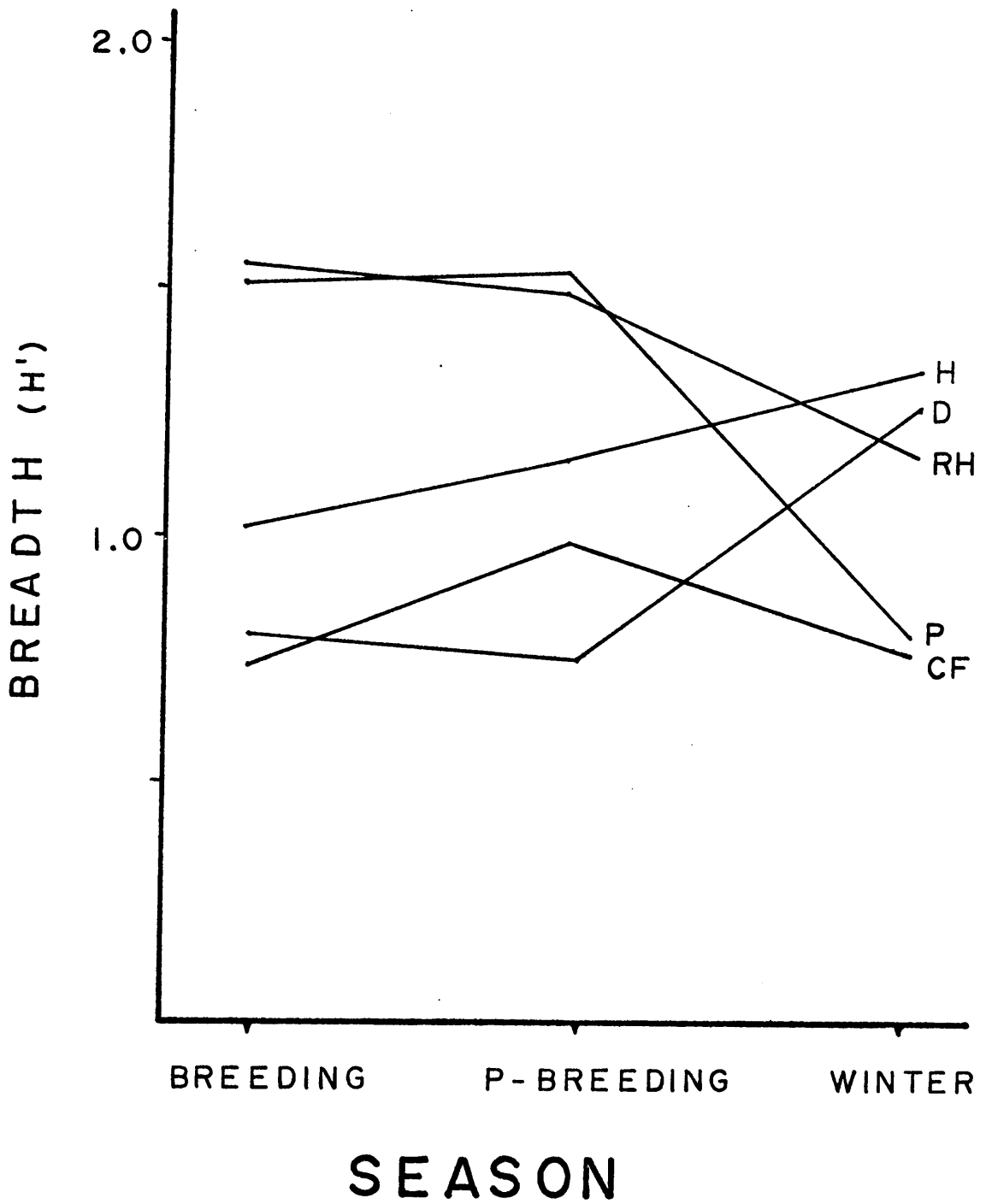


Figure 17. Breadth of the foraging methods used by five species of woodpeckers during the breeding, post-breeding, and winter seasons. (See Table 2 for species code.)

FORAGING METHODS



different woodpeckers. Pileated woodpeckers fed mainly on carpenter ant pupae and adults during the winter. Carpenter ant galleries are most often found in the lower portions of tree trunks. The only method to gain access to these chambers is by excavation. Thus pileated woodpeckers tend to concentrate on lower portions of tree trunks and excavate most of the time resulting in a decrease in breadth of micro-habitat and foraging methods used (Figs. 16, 17).

In contrast, downy woodpeckers typically forage superficially and cannot reach concentrated areas of food like pileated woodpeckers. When food becomes less abundant, downy woodpeckers must increase breadth in all aspects of their foraging in order to find sufficient food.

Hairy woodpeckers, with intermediate excavating capabilities between downy and pileated woodpeckers, showed an intermediate response in breadth changes. There was an increase in breadth of foraging methods and macro-habitat used but a decrease in micro-habitat (Figs. 16, 17).

Red-headed woodpeckers decreased in breadth of foraging methods used in the winter because of their heavy reliance on acorn stores (Figs. 11, 17). Common flickers foraged more on the ground in the breeding and winter seasons than in the post-breeding season (Fig. 10) causing a decrease in breadth of foraging methods used during the spring and winter (Fig. 17).

Overlap as a Function of Breadth and Similarity

If each aspect of a species' foraging behavior (methods, and micro- and macro-habitat) is considered as a hypervolume in n-dimensional space, these clouds of data points can be visualized as changing with resource availability changes, and as pressures from other species are exerted on them. The hypervolumes can expand and contract in one or more dimensions, creating changes in breadth. Centroids of the hypervolumes may also move in hyperspace (i.e. representing movement of the entire hypervolume) as a response to resource availability. Overlap between hypervolumes of two species will be a function of both directional movements of the hypervolumes and changes in breadth. For these reasons seasonal changes in breadth, Euclidean distance, and overlap must be viewed together for comparisons of species' foraging behaviors (e.g., Fig. 18).

Comparisons of Species' Overlap

Common flickers and red-headed woodpeckers have macro-habitats quite different from the downy, hairy, and pileated woodpeckers. Further evidence in support of this is the Euclidean distances (a similarity index) between centroids of species' hypervolumes of macro-habitat (Table 20). Data clouds in n-dimensional space for common flickers and red-headed woodpeckers always had a high Euclidean distance between them and those for downy, hairy, and pileated woodpeckers (Table 20), indicating a low degree of

Figure 18. Breadth, overlap, and Euclidean distance of foraging methods, micro-habitat, and macro-habitat for comparisons between the downy and hairy woodpeckers during the breeding, post-breeding, and winter seasons. (BR--breeding season, P-BR--post-breeding season, W--winter, see Table 2 for species code.)

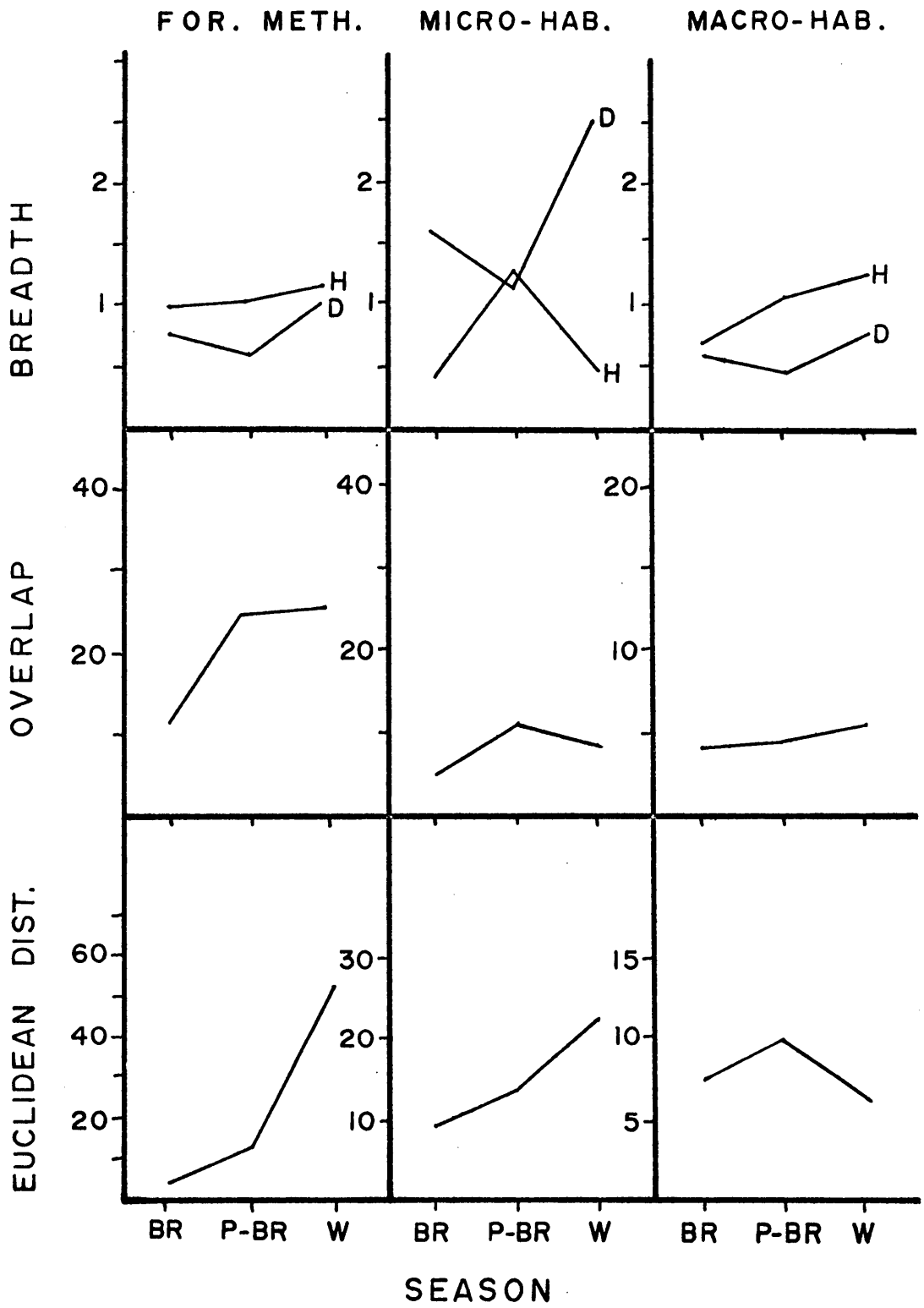


Table 20. Matrices of Euclidean distances (similarity index) between centroids of woodpecker species' macro-foraging habitat to demonstrate seasonal differences. Higher values indicate lower similarities.

Species	D	H	P	CF	RB
<u>Breeding Season</u>					
Hairy	7.4				
Pileated	13.3	11.2			
Common Flicker	38.4	33.3	43.5		
Red-bellied	13.2	18.3	11.6	51.3	
Red-headed	35.6	33.0	40.7	21.0	49.8
<u>Post Breeding Season</u>					
Hairy	10.1				
Pileated	9.1	7.3			
Common Flicker	37.4	46.3	43.6		
Red-bellied	14.4	23.1	22.7	28.3	
Red-headed	42.6	52.2	47.2	30.8	35.9
<u>Winter Season</u>					
Hairy	7.2				
Pileated	6.8	10.8			
Common Flicker	30.5	24.4	35.1		
Red-bellied	6.0	4.9	11.8	24.7	
Red-headed	42.8	38.9	46.6	25.9	37.4

similarity. Through all seasons downy, hairy, and pileated woodpeckers occupied very similar macro-habitats as indicated by small Euclidean distances (Table 20).

For the above reasons I shall deal only with the downy, hairy, and pileated woodpeckers in the analyses of overlap. Since these three species overlapped to the greatest extent in use of macro-habitat, changes in their selection of foraging methods and micro-habitat with changing resource availability should best demonstrate interactions of overlap between species and food abundance.

The relationship between Euclidean distance and overlap did not follow a pattern for any species' comparisons (Figs. 18, 19, 20). Independent changes in breadth appeared to be the main reason. It should be noted here that my measurements of breadth are results of net changes in the entire hypervolume. Changes in breadth that affect overlap (when overlap is calculated by the group discriminant analyses) are only those changes that occur in the area of minimal overlap between two hypervolumes, i.e. changes in breadth along the discriminant axis. For these reasons a direct relationship among breadth, overlap, and Euclidean distance will not always be observed.

May and MacArthur (1972) have predicted that overlap between species using similar resources should be high when resources are abundant, and low when resources are limiting. Therefore, based on my assumptions of the seasonal availability of food, overlap between foraging behaviors of woodpeckers should be least during the winter, moderate during the breeding season, and greatest during the

Figure 19. Breadth, overlap, and Euclidean distance of foraging methods, micro-habitat, and macro-habitat for comparisons between the downy and pileated woodpeckers during the breeding, post-breeding, and winter seasons. (BR--breeding season, P-BR--post-breeding season, W--winter, see Table 2 for species code.)

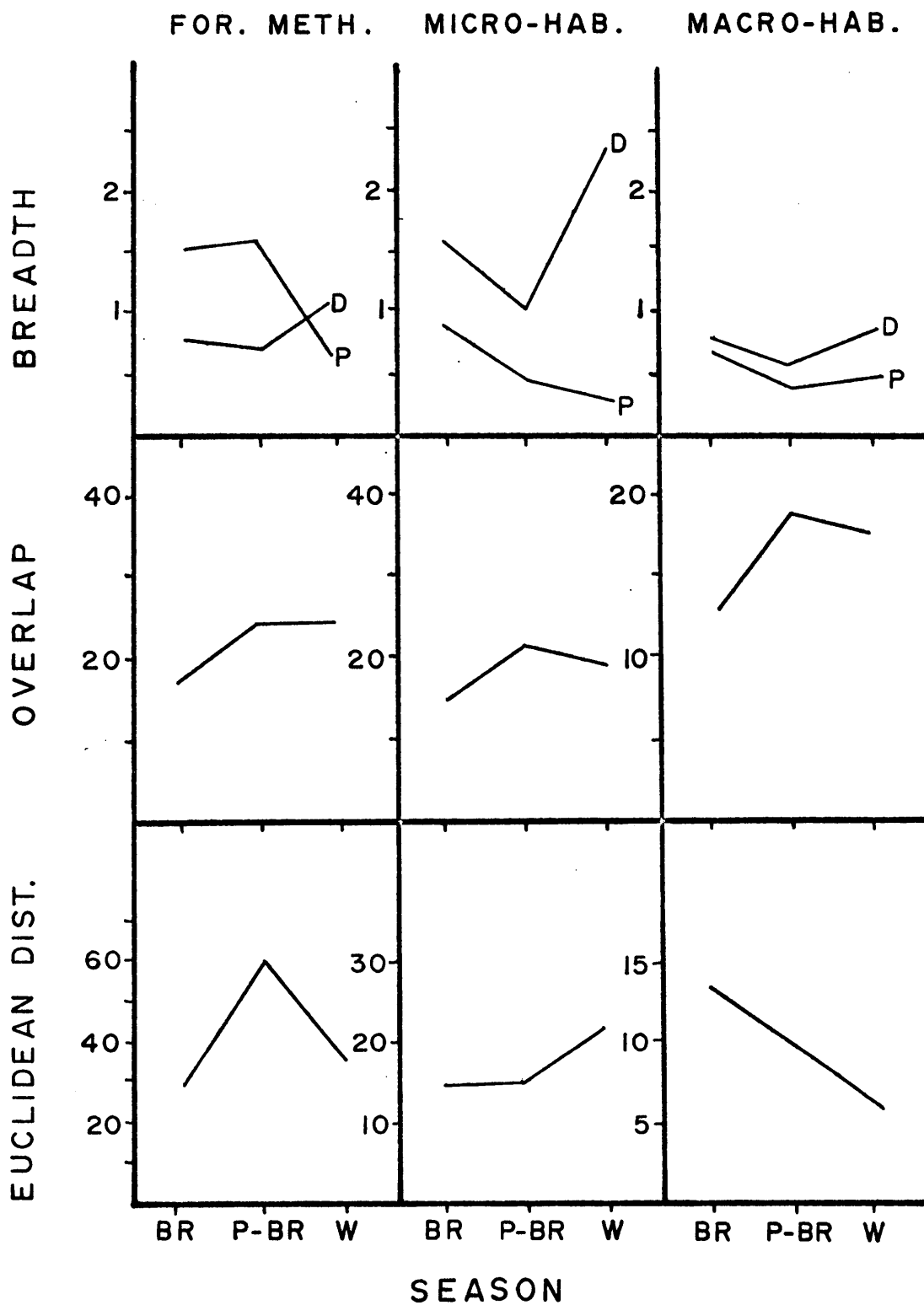
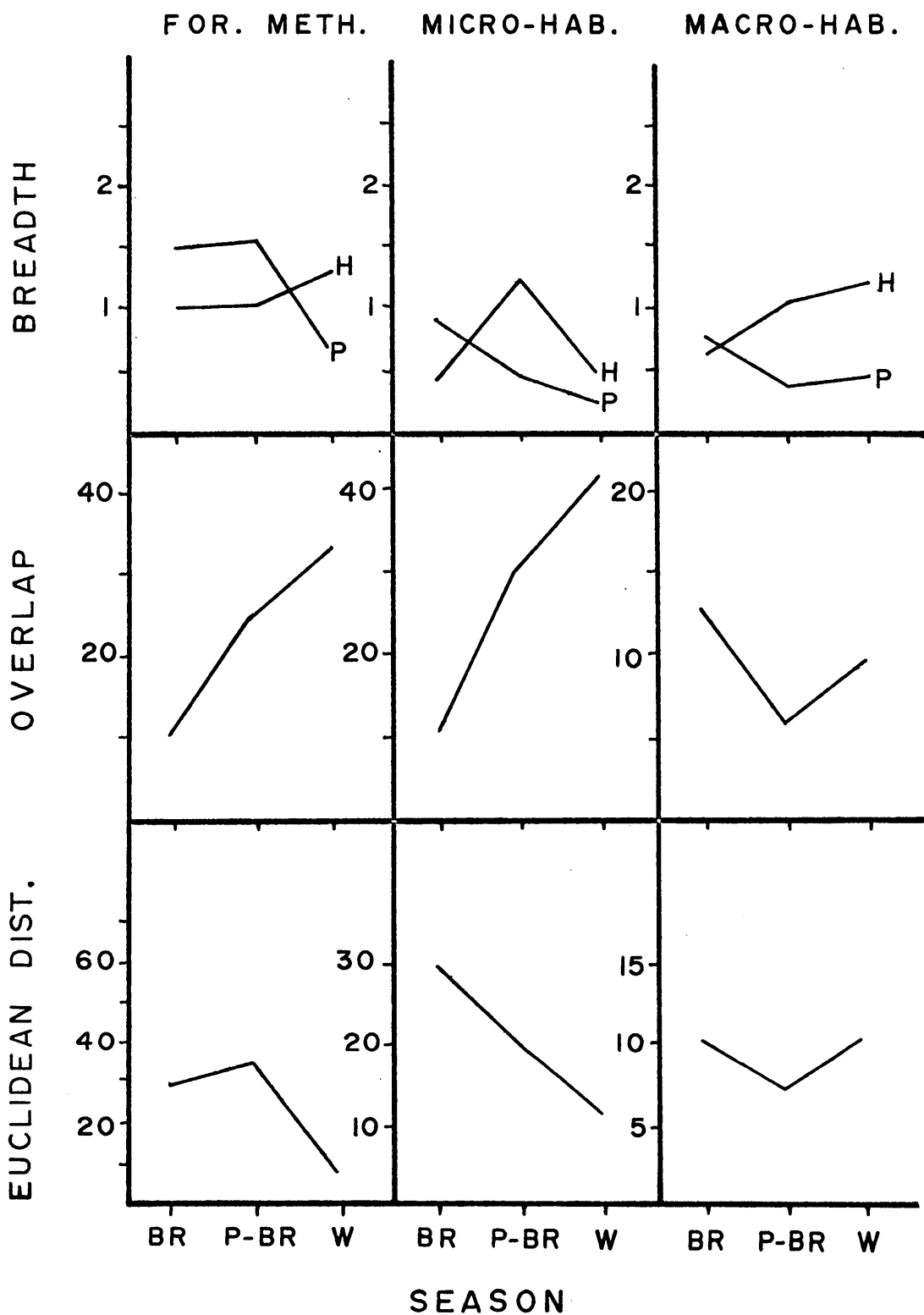


Figure 20. Breadth, overlap, and Euclidean distance of foraging methods, micro-habitat, and macro-habitat for comparisons between the hairy and pileated woodpeckers during the breeding, post-breeding, and winter seasons. (BR--breeding season, P-BR--post-breeding season, W--winter, see Table 2 for species code.)



post-breeding season. This assumes that overlap is inversely proportional to competition, and that competition is the "force" causing the reductions in overlap between species.

Downy and Hairy Woodpeckers: Downy and hairy woodpeckers overlapped the least in all three aspects of foraging behavior during the breeding season (Fig. 18). This suggests the possibility that my assumptions on resource availability may be wrong and that food resources were most limiting during the breeding season rather than winter. Formation of eggs, excavation of nest cavities, and food requirements of nestlings together create a high energy demand during the breeding season which might account for an error in my assumptions. An alternate possibility is that resources were not limiting, and that the two species were foraging on "preferred" items at "preferred" places. During the post-breeding season there was an increase in overlap of foraging methods and habitat use. This increase in all three aspects of foraging behavior would be expected since resource availability should be at a maximum allowing extensive overlap. During the winter season there was a further increase in overlap of foraging methods and macro-habitat used, but a decrease in overlap of micro-habitat (Fig. 18). As a response to a decrease in resource availability, downy and hairy woodpeckers used the same physical land area to a greater extent, and used more similar methods to feed, but selected less similar micro-habitats. Shifts in structural habitat have been reported in lizards (Anolis spp.) (Jenssen 1973, Schoener 1975).

A unique relationship appears to exist between breadth and overlap of micro-habitat for downy and hairy woodpeckers (Fig. 18). Breadth for hairy woodpeckers showed an inverse response to that for the downy woodpecker. It appears that as the downy increased breadth, as a response to a less abundant resource, hairy woodpeckers concentrated on specific aspects of the micro-habitat, resulting in a decrease in breadth. The net result was a decrease in overlap between the two species' use of micro-habitat (Fig. 18). Austin (1976) reported a similar relationship of changes in breadth between male and female ladder-backed woodpeckers.

Multivariate methods of measuring breadth and overlap, while providing a comprehensive view of interactions between species, often make it difficult to visualize which variable or variables account for multivariate changes. In light of this, I have standardized the micro- and macro-habitat data and calculated breadth for each species and overlap between species for each variable during each season (Tables 21, 22, 23, 24).

Downy woodpeckers increased in breadth of micro-habitat used between the post-breeding and winter season (Fig. 18). This was caused by an increase in breadth of all micro-habitat variables (Table 21). Hairy woodpeckers decreased in breadth (Fig. 18). This was the net result of a marked decrease in breadth of tree height and tree DBH foraged in, and an increase in breadth of heights of the woodpeckers in trees and diameters of stems used within trees (Table 21).

Table 21. Seasonal changes in variance values of standardized micro-foraging habitat variables for the downy, hairy, and pileated woodpeckers. (See Table 1 for mnemonic variable codes.)

Variable	Downy	Hairy	Pileated	Downy Male	Downy Female	Hairy Male	Hairy Female
<u>Breeding Season</u>							
WHGT	0.704	0.176	0.552	0.043	0.744	0.241	0.098
SDIA	0.618	0.445	1.231	2.127	0.579	0.255	1.117
THGT	0.598	0.216	0.599	0.510	0.634	0.260	0.202
TDBH	0.878	0.145	0.270	0.046	0.928	0.086	0.198
<u>Post-breeding Season</u>							
WHGT	0.369	0.718	0.296	0.280	0.425	0.417	0.807
SDIA	0.467	0.343	0.934	0.145	0.472	0.244	0.397
THGT	0.465	0.976	0.219	0.290	0.517	0.333	1.200
TDBH	0.554	0.759	0.130	0.663	0.507	0.470	0.785
<u>Winter Season</u>							
WHGT	0.877	0.801	0.385	0.815	0.927	0.265	0.939
SDIA	0.761	0.346	0.369	0.013	0.667	0.402	0.306
THGT	0.590	0.567	0.471	0.645	0.474	0.419	0.607
TDBH	1.266	0.396	0.118	0.826	1.509	0.107	0.496

Table 22. Seasonal changes in variance values of standardized macro-foraging habitat variables for the downy, hairy, and pileated woodpeckers. (See Table 1 for mnemonic variable codes.)

Variable	Downy	Hairy	Pileated	Downy Male	Downy Female	Hairy Male	Hairy Female
<u>Breeding Season</u>							
BA	0.417	0.871	0.891	0.405	0.406	1.108	0.510
DOS	0.618	0.703	0.760	0.712	0.586	0.590	0.792
CH	0.473	0.502	0.390	0.334	0.605	0.544	0.513
<u>Post-breeding Season</u>							
BA	0.515	0.562	0.295	0.612	0.372	0.445	0.673
DOS	0.530	1.226	0.278	0.653	0.411	0.814	1.472
CH	0.407	0.619	0.250	0.495	0.356	0.362	0.832
<u>Winter Season</u>							
BA	0.612	0.992	0.522	0.741	0.535	1.384	0.641
DOS	1.077	1.741	0.783	1.115	1.104	2.651	0.767
CH	0.552	0.803	0.366	0.604	0.531	0.664	0.837

Table 23. Seasonal changes in linear overlap of standardized micro-foraging habitat variables for the downy, hairy, and pileated woodpeckers. (See Table 1 for mnemonic variable codes.)

Variable	D and H	D and P	H and P	D Male and D Female	H Male and H Female
<u>Breeding Season</u>					
WHGT	1.32	2.04	1.32	0.69	1.20
SDIA	1.92	1.84	1.47	2.07	2.00
THGT	1.48	2.14	1.48	0.92	1.38
TDBH	0.99	1.42	0.58	0.69	1.18
<u>Post-breeding Season</u>					
WHGT	2.32	1.92	1.65	2.06	1.85
SDIA	2.61	2.62	2.60	1.29	1.77
THGT	2.90	1.49	1.49	1.85	1.60
TDBH	2.92	1.13	1.13	2.34	2.09
<u>Winter Season</u>					
WHGT	3.21	2.32	2.55	2.95	1.56
SDIA	2.80	1.34	2.14	0.36	1.80
THGT	2.98	2.59	2.63	2.33	2.15
TDBH	2.53	1.39	1.39	3.18	1.12

Table 24. Seasonal changes in linear overlap of standardized macro-foraging habitat variables for the downy, hairy, and pileated woodpeckers. (See Table 1 for mnemonic variable codes.)

Variable	D and H	D and P	H and P	D Male and D Female	H Male and H Female
<u>Breeding Season</u>					
BA	2.07	2.04	3.10	2.06	2.03
DOS	2.66	2.82	2.66	2.18	2.14
CH	2.14	2.55	2.14	1.96	1.76
<u>Post-breeding Season</u>					
BA	2.73	1.31	1.93	1.77	2.19
DOS	2.34	1.24	1.47	2.06	3.06
CH	2.30	1.35	1.35	1.56	1.80
<u>Winter Season</u>					
BA	2.82	2.70	2.42	1.88	2.23
DOS	3.22	3.06	3.34	3.22	2.11
CH	2.61	2.51	2.58	2.10	2.00

Interactions of variables as they affected changes in breadth of macro-habitat can be determined in Table 22.

Changes in overlap cannot be traced back to the original variables as easily as changes in breadth. Overlap of micro- and macro-habitats were measured on a discriminant axis which may not have any orientation relationships to any of the original axes. Seasonal changes in magnitude of individual variables may not reflect changes in minimal overlap. Nonetheless, some information can be obtained from overlap values for each variable. The downy and hairy woodpecker overlapped the least in tree DBH used in the breeding season, height of the woodpecker above the ground in the post-breeding season, and tree DBH used again in the winter (Table 23). These were the variables of lowest overlap for their respective seasons. Similar comparisons can be made for macro-habitat using Table 24. Tables 21, 22, 23, and 24 may be used by readers if they wish to make future comparisons of breadth and overlap with the original variables.

Downy and Pileated Woodpeckers: Changes in overlap between downy and pileated woodpeckers were quite close to what would be expected. Overlap was the least for all aspects of foraging behavior during the breeding season (Fig. 19). This was also observed in the comparison between downy and hairy woodpeckers (Fig. 18), and suggests again the possibility of an error in my assumption of food availability because of the presence of high energy demands on nesting woodpeckers. Overlap increased in all areas during the post-breeding season as might be expected because of an increase in food availability. During

winter, overlap in micro- and macro-habitat decreased while overlap in foraging methods remained about the same (Fig. 19). This would be expected since the food resources should decrease in abundance during the winter.

When comparing the overlap between downy and hairy woodpeckers (Fig. 18) with the overlap between downy and pileated woodpeckers (Fig. 19), the expected relationship is not observed. Since downy and hairy woodpeckers are congeners and have the most similar foraging behaviors, I would have expected them to show a stronger response in overlap changes than comparisons between the downy and pileated; the reverse was observed (Figs. 18, 19).

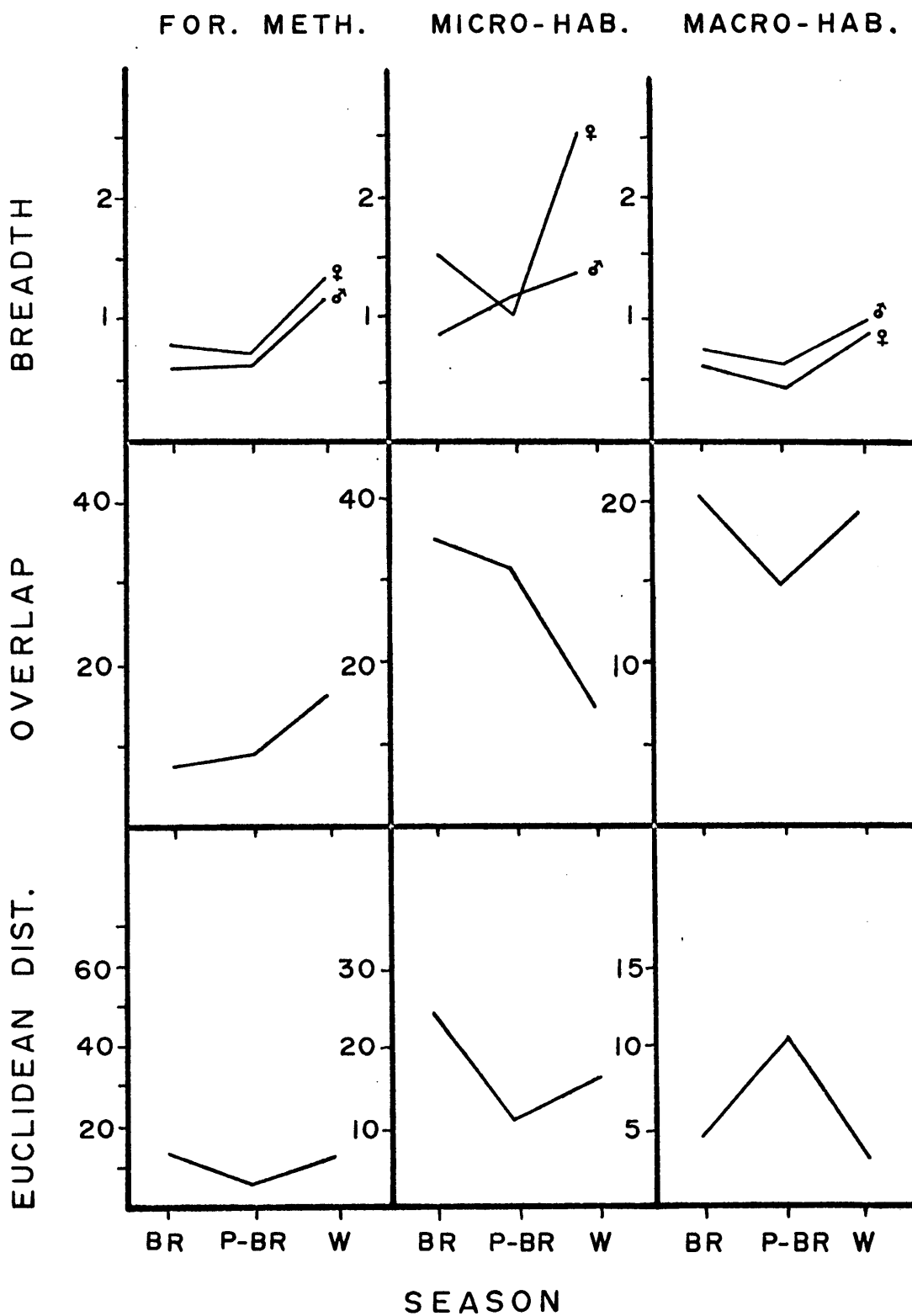
Hairy and Pileated Woodpeckers: Seasonal changes in overlap between hairy and pileated woodpeckers conformed in part to what was expected (Fig. 20). During the breeding season the two species overlapped the most in the macro-habitats they used, and the least in foraging methods and micro-habitat (Fig. 20). During the post-breeding season overlap between the two species in foraging methods and micro-habitat increased greatly, while use of macro-habitats became less similar (Fig. 20). Overlap between the hairy and pileated woodpeckers during the winter increased in all three areas examined (Fig. 20). This was quite unexpected as the abundance of food in winter should have decreased. This discrepancy suggests the possibility that there may have been a considerable ecological distance between these two species, and that the scarcities of food in winter may have forced the two

species to use a relatively unused portion of the resource, e.g. food items obtained only through extensive excavations.

Comparisons of Overlap and Breadth Between Sexes

Overlap: During the breeding season male and female downy woodpeckers overlapped the most in macro- and micro-habitat, but overlapped the least in foraging methods (Fig. 21). This indicates that they foraged in similar places but sought different food items. In the post-breeding season they foraged in less similar macro- and micro-habitats, but used foraging methods that were more similar (Fig. 21). The greatest changes in overlap occurred in the winter. The two sexes foraged in more similar macro-habitats and overlapped the most in foraging methods (Fig. 21). Overlap in micro-habitat, however, decreased greatly. Male and female downy woodpeckers increased both the breadth of macro-habitat and foraging methods used (Fig. 21), probably as a response to a decrease in the density of food. This coupled with shifts in Euclidean distance between the hypervolumes caused the increases in overlap of their macro-habitat and foraging methods. Overlap was reduced by males and females foraging in different micro-habitats (Fig. 21), mainly by foraging on different diameter stems (Table 23). The fact that the greatest changes in overlap occurred during the winter may indicate that in winter food resources are more limiting between male and female downy woodpeckers than the breeding season.

Figure 21. Breadth, overlap, and Euclidean distance of foraging methods, micro-habitat, and macro-habitat for comparisons between male and female downy woodpeckers during the breeding, post-breeding, and winter seasons. (BR--breeding season, P-BR--post-breeding season, W--winter, see Table 2 for species code.)

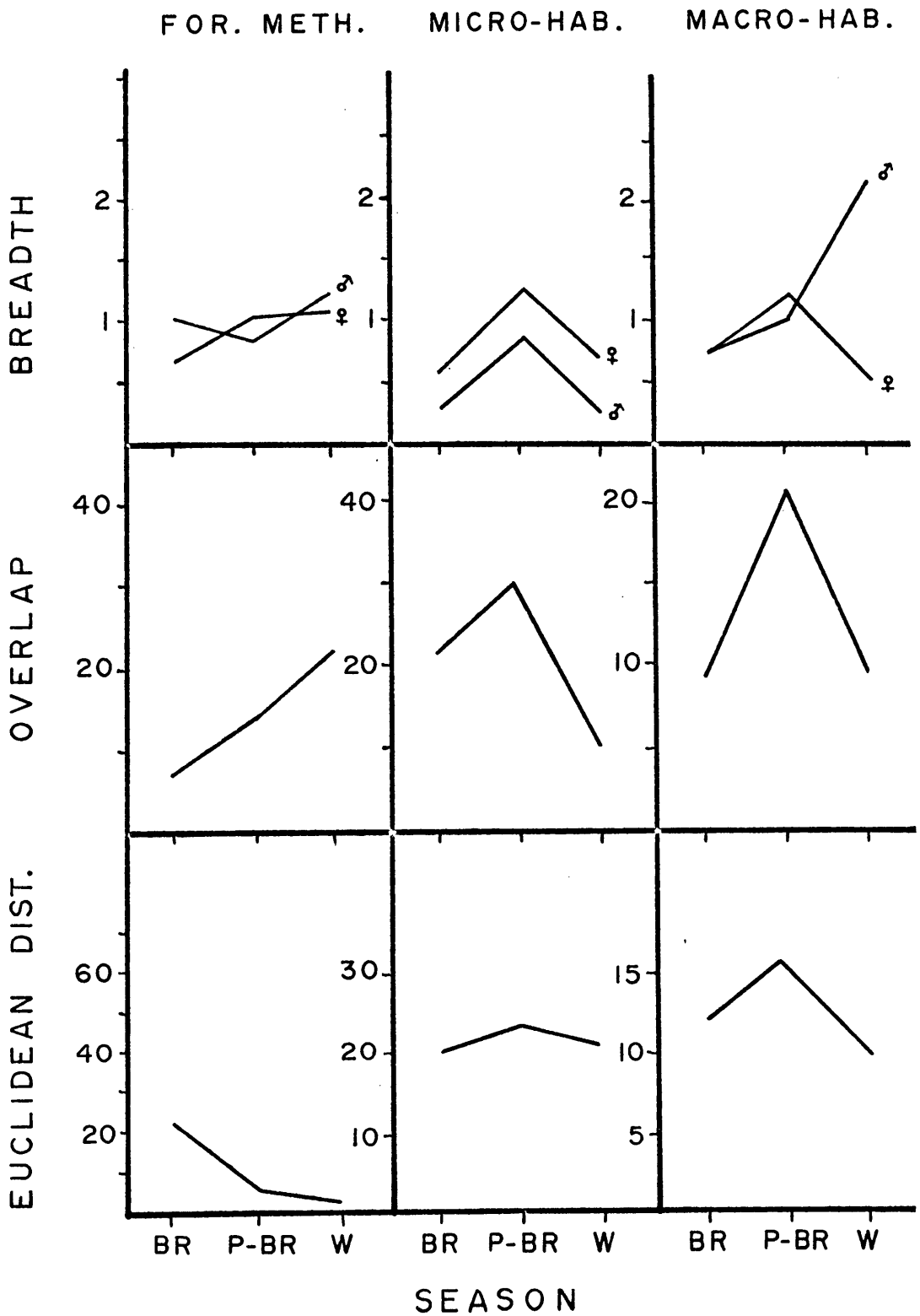


Hairy woodpeckers responded as though food were limiting in both the breeding season and winter (Fig. 22). Overlap in foraging methods and macro-habitat was lowest between male and female hairy woodpeckers during the breeding season. All three aspects of foraging behavior showed an increase in overlap in the post-breeding season (Fig. 22). Since food was assumed to be plentiful during this season, this increase was expected. In the winter, males and females overlapped the most in foraging methods (Fig. 22), as did male and female downy woodpeckers (Fig. 21), while overlap of micro- and macro-habitat showed a great decrease (Fig. 22). This probably represents an overall decrease in overlap as a response to a decrease in food abundance.

Breadth: On the whole sexes were quite similar in changes in breadth between seasons, but there were some exceptions. Downy woodpecker males and females showed very similar values and nearly parallel seasonal changes in breadth of foraging methods and macro-habitat (Fig. 21). With the post-breeding season excepted, males showed less breadth than females in use of micro-habitat.

Male and female hairy woodpeckers were quite similar in breadth of foraging methods and micro-habitat, but not in breadth of macro-habitat (Fig. 22). Breadth of macro-habitat was quite similar for the breeding and post-breeding seasons, but diverged widely in the winter when males selected a more diverse macro-habitat than did females (Fig. 22).

Figure 22. Breadth, overlap, and Euclidean distance of foraging methods, micro-habitat, and macro-habitat for comparisons between male and female hairy woodpeckers during the breeding, post-breeding, and winter seasons. (BR--breeding season, P-BR--post-breeding season, W--winter, see Table 2 for species code.)

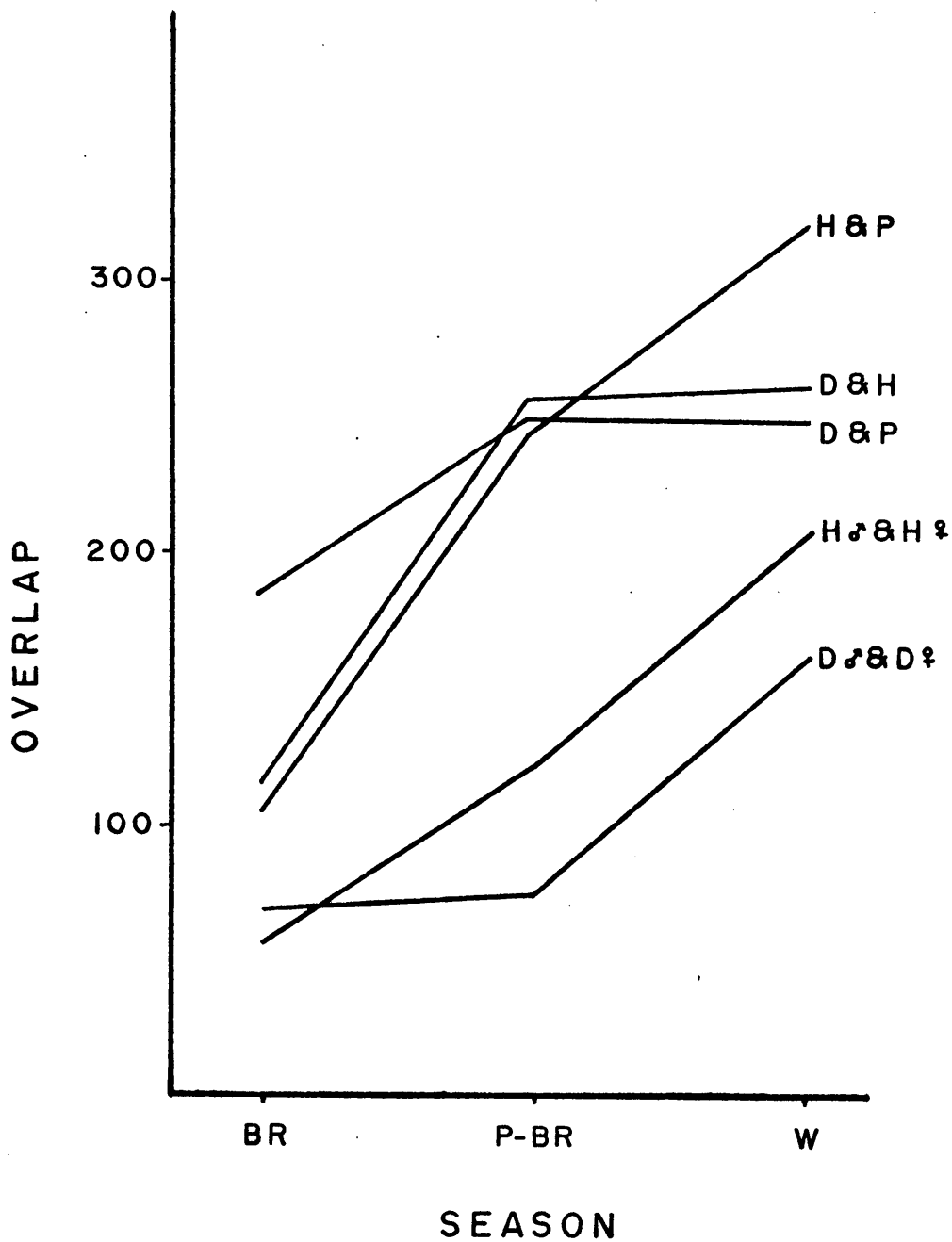


A Comparison of Overlap Between Species with Overlap Between Sexes

Overlap between foraging methods was calculated by summing overlap between groups on each axis of the same principal component analysis allowing overlap between groups to be compared. Overlap between groups for micro- and macro-foraging habitat cannot be compared since each pair comparison was calculated by a separate discriminant analysis.

Since different sexes of a species are more similar genetically than different species, one might expect to find that males and females of the same species overlap more in foraging methods than different species do. This was not the case. If each season is examined separately, the sexes of downy and hairy woodpeckers overlapped less than all the other species pair comparisons (Fig. 23). This suggests that selective pressures causing differences in foraging methods between male and female downy and hairy woodpeckers, are greater than those causing differences between the species pair examined.

Figure 23. Overlap of woodpecker foraging methods during the breeding, post-breeding, and winter seasons. (See Table 2 for species code.)



SUMMARY AND CONCLUSIONS

The six woodpeckers examined partitioned the food resource by selecting different foraging methods and habitats. Common flickers and red-headed woodpeckers differed greatly from the other species in their selection of micro-habitat and foraging methods. Flickers also selected a much different micro-habitat by foraging extensively on the ground. Downy, hairy, and pileated woodpeckers overlapped a great deal in all aspects of foraging behavior examined. However, when differences within the three aspects of behavior (selection of macro- and micro-habitats and foraging methods) were summed, there were substantial differences among these three species. The three species concentrated their foraging activities on different parts of trees as well as using different regimes of foraging methods.

Differences in foraging behavior were also observed between sexes of downy and hairy woodpeckers. These differences were confined mainly to selection of micro-habitat and foraging methods. No differences in foraging behavior were detected between male and female common flickers.

It is suggested that bill and body size of downy, hairy, and pileated woodpeckers may be related more to the depth to which each species penetrates trees when foraging rather than to prey or food size as has been suggested in other species by Schoener (1965), Hespenheide (1966), and Diamond (1973).

Seasonal changes in foraging methods of woodpeckers were observed. Downy, hairy, and pileated woodpeckers used subcambial foraging methods to a greater extent in the winter than in the breeding and post-breeding seasons. This was probably a response to the location of prey items at different seasons. Food items were apparently more superficially available during the breeding and post-breeding season than in the winter. Red-headed woodpeckers responded to the winter food shortage by feeding on acorns collected and stored in the previous season. Many of the common flickers avoided winter shortages by migrating out of the area as the population density of flickers was greatly reduced in the winter from the levels present in the breeding and post-breeding seasons. All species altered their selection of types of food items during the winter.

Downy, hairy, and pileated woodpeckers showed varied responses to changing resource availability in their breadths of foraging methods, and micro- and macro-habitats used (Table 25). Predicted changes in breadth indicate that breadth should increase as the food resource becomes less dense, and decrease as the resource becomes more dense (MacArthur and Pianka 1966; Emlen 1966, 1968; MacArthur and Levins 1967). However, downy woodpeckers were the only species to fit the predicted response pattern for all aspects of foraging behavior examined (Table 25). Pileated woodpeckers decreased in breadth of foraging methods and micro-habitats used during the winter. Since the pileated woodpecker fed mostly on carpenter ant adults and pupae (a concentrated food source) during the winter, their low breadth of

Table 25. Summary of predicted versus observed changes in species' breadth. INC (increasing breadth) and DCR (decreasing breadth) indicate theoretically predicted trends, while + (agreement) and - (disagreement) indicate whether observed trends agreed with those predicted. (B: breeding season, PB: post-breeding season, W: winter)

	<u>Downy</u>		<u>Hairy</u>		<u>Pileated</u>	
	<u>B to PB</u>	<u>PB to W</u>	<u>B to PB</u>	<u>PB to W</u>	<u>B to PB</u>	<u>PB to W</u>
Predicted	DCR	INC	DCR	INC	DCR	INC
<u>Variable Set</u>						
Foraging Methods	+	+	-	+	-	-
Micro- Habitat	+	+	-	-	+	-
Macro- Habitat	+	+	-	+	+	+
Probable Net Result	+	+	-	+	+	-

foraging methods and micro-habitat used may actually fit the predictions. In a localized area, the pileated woodpeckers' main winter food source is really quite dense: thus breadth might be expected to decrease. The response of breadth to resource availability for hairy woodpeckers was intermediate between those of downy and pileated woodpeckers, suggesting that densities of their winter food resources might be intermediate to those of the two other species. Downy woodpeckers foraged more superficially than hairy and pileated woodpeckers and probably encountered a very sparse, low density food resource. Hence, they responded closely to what was predicted.

I assumed that resources would be most limiting during the winter. This may not have been the case since the least overlap between downy, hairy, and pileated woodpeckers for the three areas examined (foraging methods, micro-habitat, and macro-habitat) occurred in the breeding season. High energy requirements during the nesting season for egg production, nest excavation, and feeding of nestlings may have put an additional stress on the food resource and caused an error in my assumption.

A summary of the observed changes of overlap between species compared favorably with those predicted by May and MacArthur (1972) (Table 26). Overlap between species typically increased during the post-breeding season; a time when food abundance should be high and energy requirements low (Table 26). Net overlap between downy and pileated woodpeckers decreased in the winter from what it had been during the post-breeding season. Overlap between hairy and pileated

Table 26. Summary of predicted versus observed changes in overlap between species. INC (increasing overlap) and DCR (decreasing overlap) indicate theoretically predicted trends, while + (agreement), - (disagreement), and o (unable to determine) indicate whether observed trends agreed with those predicted. (B: breeding season, PB: post-breeding season, W: winter)

Predicted	<u>Downy & Hairy</u>		<u>Downy & Pileated</u>		<u>Hairy & Pileated</u>	
	B to PB	PB to W	B to PB	PB to W	B to PB	PB to W
	INC	DCR	INC	DCR	INC	DCR
<u>Variable Set</u>						
Foraging Methods	+	-	+	o	+	-
Micro- Habitat	+	+	+	+	+	-
Macro- Habitat	+	-	+	+	-	-
Net Result	+	o	+	+	+	-

woodpeckers, however, increased in all three aspects of foraging behavior examined, suggesting the possibility that some unused "ecological space" existed between these two species, allowing their foraging behaviors to become more similar in the winter. An alternate possibility is that they selected extremely different food items in the winter, allowing extensive overlap in the areas I examined. I was unable to determine what food items were eaten as I did not shoot birds and analyze stomach contents.

If the low degree of overlap between species during the breeding season and the increase in overlap during the post-breeding season was a response to resource availability, I suggest that the changes in overlap were the result of competition between the species in the past. Seasonal changes in overlap between male and female downy and hairy woodpeckers lend additional support to this idea. Male and female downy woodpeckers showed a great decrease in overlap of micro-foraging habitat during the winter. Male and female hairy woodpeckers overlapped least in the breeding and winter seasons and most in the post-breeding season; a perfect response if varying degrees of competition were the cause of the changes in overlap. Both hairy and downy woodpeckers are sexually dimorphic in bill sizes. Willson et al. (1975) have suggested that sexual dimorphism in bill size may occur more often in a species where food is limiting than in species where food is not limiting.

Overlap of foraging methods in species pair comparisons of the downy, hairy, and pileated woodpeckers was greater than that between

sexes of downy and hairy woodpeckers. This suggests that selective pressures causing differences in foraging methods between sexes may be greater than those between species for the groups examined.

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SEASONAL CHANGES IN THE FORAGING METHODS AND HABITATS OF SIX
SYMPATRIC WOODPECKER SPECIES IN SOUTHWESTERN VIRGINIA

by

Richard Neil Conner

(ABSTRACT)

Foraging methods and habitats used by downy, hairy, pileated, red-bellied, and red-headed woodpeckers, and common flickers were studied in southwestern Virginia during the breeding season, post-breeding season, and winter. The food resource used by the six species was partitioned by species' use of different macro-habitats (forest structure), micro-habitats (positions within trees), and foraging methods. Differences in foraging behaviors of male and female downy and hairy woodpeckers were also detected.

Seasonal changes in foraging methods of woodpeckers were observed. Downy, hairy, and pileated woodpeckers used subcambial foraging methods to a greater extent in the winter than in the breeding and post-breeding seasons. This was probably a response to the location of prey items at different seasons. Food items were apparently more superficially available during the breeding and post-breeding season than in the winter. Red-headed woodpeckers responded to the winter food shortage by feeding on acorns collected and stored in the previous season. Many of the common flickers avoided winter

shortages by migrating out of the area as the population density of flickers was greatly reduced in the winter from the levels present in the breeding and post-breeding seasons.

It is suggested that bill and body size of downy, hairy, and pileated woodpeckers may be related more to the depth to which each species penetrates trees when foraging rather than to prey or food size as has been suggested in other species.

Downy, hairy, and pileated woodpeckers showed varied responses to changing resource availability in their breadths of foraging methods and micro-habitat used. Predicted changes in breadth indicate that breadth should increase as the food resource becomes less dense, and decrease as the resource becomes more dense. Downy woodpeckers were the only species to fit the predicted response pattern for all aspects of foraging behavior examined. Pileated woodpeckers decreased in breadth of foraging methods and micro-habitats used during the winter.

Net overlap between downy and hairy, and downy and pileated woodpeckers decreased in the winter from what it had been during the post-breeding season. Overlap between hairy and pileated woodpeckers, however, increased in all three aspects of foraging behavior examined suggesting the possibility that some unused "ecological space" existed between these two species allowing their foraging behaviors to become more similar in the winter. It is suggested that changes in overlap were the result of competition in the past.

Pressures causing differences in foraging methods between sexes may be greater than those between species for the groups examined. Overlap of foraging methods in species pair comparisons of the downy, hairy, and pileated woodpeckers was greater than that between sexes of downy and hairy woodpeckers.