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FORAGING DIFFERENCES AMONG FEMALE AND MALE DOWNY AND HAIRY WOODPECKERS

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Partitioning of foraging resources is generally thought to be the result of past competition among sympatric (co-occurring) species with similar life history strategies (Roughgarden 1976; Pacala and Roughgarden 1982a, 1982b). Numerous examples exist of intraspecific resource partitioning through sexual differences in foraging behaviors of Downy *(Picoides pubescens)*, but few for Hairy *(P. villosus)* woodpeckers (Kilham 1965, 1970, 1983; Jackson 1970; Willson 1970, Kisiel 1972; Peters and Grubb 1983). Male Downy Woodpeckers tend to forage on small branches regardless of height (Conner 1977), whereas females forage on tree trunks and larger limbs (Jackson 1970). Male and female Hairy Woodpeckers tend to forage on different substrates independent of the position of the foraging substrate in New York (Kisiel 1972); in Virginia however, females foraged higher in trees than males (Conner 1977).

Conspecific pairs of *Picoides* woodpeckers often forage in closer proximity to each other than they do with other woodpecker species. If competition intensity is the primary natural selective pressure that results in resource partitioning, pairs of *Picoides* woodpeckers might exhibit greater resource partitioning than that observed between species. Downy and Hairy woodpeckers offer an excellent opportunity to explore intra- and interspecific overlap of foraging behaviors with two sympatric species.

Kisiel (1972) investigated foraging behavior similarities among female and male, Downy and Hairy woodpeckers. His results suggested that overlap between female and male Hairy Woodpeckers was similar to interspecific overlap with Downy Woodpeckers. Foraging behavior of female and male Downy Woodpeckers, however, appeared to overlap less than interspecific comparisons. The "single variable at a time" approach (univariate) to measures of overlap used in his study makes interpretation of niche relationships among species and sexes quite difficult.

Between 1972 and 1976 I studied woodpecker foraging ecology in the central Appalachian Mountains (Conner 1979, 1980, 1981). Although the primary focus of that research was to compare niche dynamics among six species of sympatric woodpeckers, data on sexual differences in the foraging behaviors of Downy and Hairy woodpeckers were also collected. In the present study I use a multivariate approach to examine intra- and interspecific foraging resource overlap among foraging female and male, Downy and Hairy woodpeckers.

STUDY AREA AND METHODS

Foraging behavior of Downy and Hairy woodpeckers was studied on a 20 km^2 area on the upper drainages of Craig and Poverty creeks on the Jefferson National Forest in southwestern Virginia. Oaks *(Quercus* spp.*)* and hickories *(Carya* spp.*)* covered 60 percent of the area; oaks and pines *(Pinus* spp.*)* covered another 20 percent. Yellow-

poplar *(Liriodendron tulipifera)*, white oak *(Q. alba)*, and northern red oak *(Q. rubra)* stands, and Virginia *(P. virginiana)*, white *(P. strobus)*, and pitch *(P. rigida)* pine stands each occupied about 10 percent of the area. A wide range of cover types and successional stages resulting from even-aged timber management was present.

Foraging behavior and habitat use of female and male, Downy and Hairy woodpeckers were measured from 1972 through 1976 during the breeding season (15 April through 15 June), post-breeding season (July through October), and winter (December through February). Because sample sizes were small, seasonal comparisons could not be made. All available cover types and stand conditions (age classes) were searched for foraging woodpeckers. Stands searched included all stages of forest succession, forest edge habitat, and agricultural areas adjacent to forest habitat. When foraging woodpeckers were located, I noted foraging methods (Appendix Table 1, Conner 1979, page 83), position within the tree (upper, middle, and lower third), general stem size (twig, branch, limb, trunk), substrate foraged upon (dead, live, or dead portion of live tree), and the micro- and macro-foraging habitat where foraging occurred (Appendix Table 1). Standardized height of a foraging woodpecker was calculated by dividing the height of the woodpecker by height of the tree and multiplying by 100. Habitat data were collected immediately after observing foraging woodpeckers. A sample unit for statistical analyses comprised the behavior and habitat position of each woodpecker at my initial contact. After collecting behavioral and habitat data on an individual woodpecker, I moved to another location (200+ m) before searching for another woodpecker. Thus, the likelihood of observing the same woodpecker more than once was extremely low. Overlap of woodpecker foraging methods during each season was calculated using Horn's $\underline{R}_o$ (1966). Overlap of woodpecker use of structural habitat was determined using the minimal density overlap method as developed by Harner and Whitmore (1977). A two-group discriminant function analysis was calculated for each species/sex pair combination for each season. I used a $\underline{z}$-distribution of standardized canonical variates to measure linear overlap, reduced by the multivariate discriminant analyses to a single dimension. This measure of overlap permitted close examination of relative differences in the structural micro- and macro-habitats used by these woodpeckers. I considered that valid comparisons of relative overlap magnitude among groups (species and sexes) can only be made within a habitat category (foraging macro- and micro-habitat, and foraging methods) and not between categories because of the different variables and methods used to measure overlap among the categories. Seasonal measures of overlap within foraging methods and habitat categories were averaged because there were no seasonal differences in relative magnitude or pattern of overlap values.

RESULTS

Female and male Downy and Hairy woodpeckers selected very similar forest structure (foraging macro-habitat) as foraging sites with one exception (Table 1, page 76). Male Hairy Woodpeckers foraged in habitats with higher basal areas of trees than did male Downy Woodpeckers. Both sexes of both species foraged in stands with similar trees densities and canopy heights.

Woodpeckers varied more in their use of different limb sizes and heights and positions in trees (foraging micro-habitat) than in their selection of forest stands (Table

2). Female Hairy Woodpeckers foraged significantly higher than did other species-sex groups. Downy Woodpeckers exhibited both intra- and interspecific differences in their selection of stem diameters for foraging, whereas female and male Hairy Woodpeckers foraged on similarly-sized stems (Table 2). Female Hairy and Downy woodpeckers foraged significantly higher (P 0.05) than did their respective males. Female woodpeckers also tended to use larger diameter trees than the males.

TABLE 1. *Intraspecific comparisons of means (SE) for Downy and Hairy woodpecker foraging macro-habitat variables.*

Variable	Downy male (N=32)	Downy female (N=42)	Hairy male (N=29)	Hairy female (N=30)
Basal area[1] (m^2/ha)	14.0 (1.5)[a]	18.3 (1.3)[a,b]	19.3 (2.0)[b]	17.7 (1.8)[a,b]
Density of stems[2] (# per 1.25 ha)	33.0 (4.0)	39.0 (3.1)	44.5 (5.2)	34.6 (4.9)
Canopy height[2] (m)	17.3 (1.2)	19.3 (1.1)	15.5 (1.3)	17.9 (1.6)

[1] Means with common letters are not significantly different, ANOVA and Duncan's new multiple range test, P < 0.05.
[2] No significant differences detected among means.

Additional insight into Downy and Hairy woodpecker use of foraging micro-habitat can be seen in the relative positions female and male woodpeckers used in trees and the types of substrate selected for foraging (Fig. 1, p. 77). Male Hairy Woodpeckers used primarily trunks and limbs as foraging sites whereas females selected limbs and branches most often (Fig. 1a). Similar to the observations of Jackson (1970), Kisiel (1972), and

TABLE 2. *Intraspecific comparisons of means (SE) for Downy and Hairy woodpecker foraging micro-habitat variables.*

Variable	Downy male (N=43)	Downy female (N=97)	Hairy male (N=45)	Hairy female (N=56)
Woodpecker[1] height (m)	8.0 (0.8)[a]	9.1 (0.7)[a]	8.6 (0.7)[a]	13.2 (0.9)[b]
Stem diameter (cm)	3.6 (0.9)[a]	15.6 (1.0)[b]	11.9 (1.1)[c]	12.1 (1.1)[c]
Tree height (m)	12.4 (1.0)[a]	16.8 (0.8)[b]	15.0 (0.9)[a,b]	20.4 (1.3)[c]
Tree DBH (cm)	36.7 (4.0)[a,b]	42.2 (3.2)[a,c]	27.8 (2.5)[b]	48.5 (3.3)[c]
Standardized woodpecker height (%)	65.7 (3.5)[a]	51.3 (2.3)[b]	56.3 (3.2)[b,c]	64.3 (2.5)[a,c]

[1] Means with common letters are not significantly different, ANOVA and Duncan's new multiple range test, P < 0.05.

FIGURE 1. *Comparisons of female and male Downy and Hairy woodpecker foraging positions (a), relative heights (b), and substrate selection (c) in southwestern Virginia.*

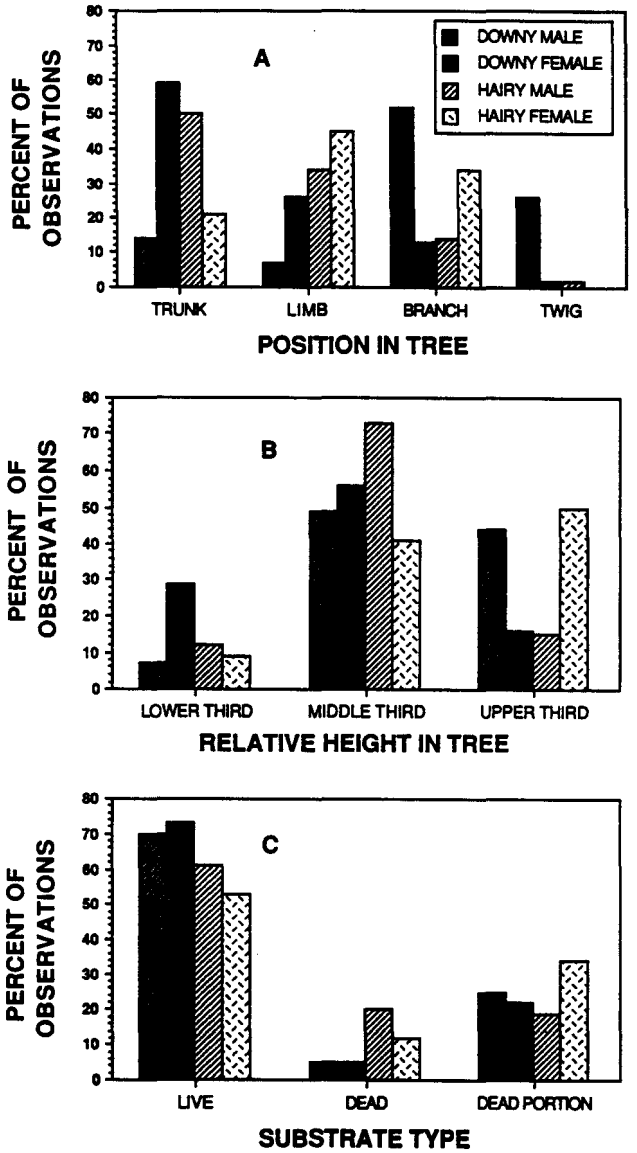


FIGURE 2. *Comparison of foraging methods used by female and male Downy and Hairy woodpeckers in southwestern Virginia (PEPO: peer-and-poke gleaning on trees, PECK: pecking on trees, SCAL: scaling bark, EXCA: subcambial excavation on trees, HAWK: hawking insects in the air, VEGF: eating vegetable material, GRDF: foraging on the ground).*

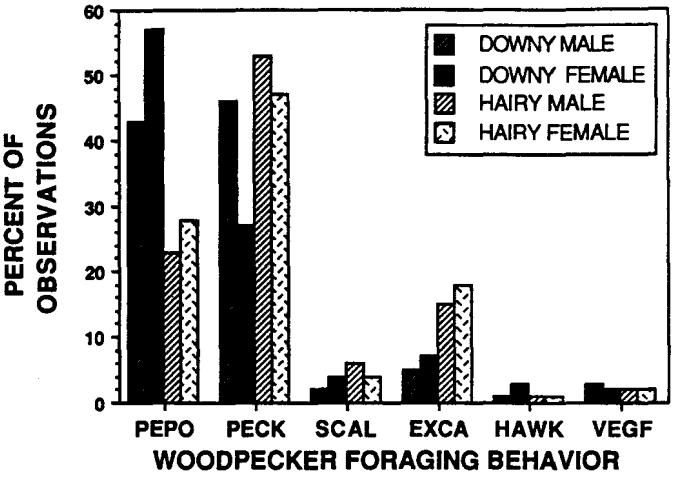
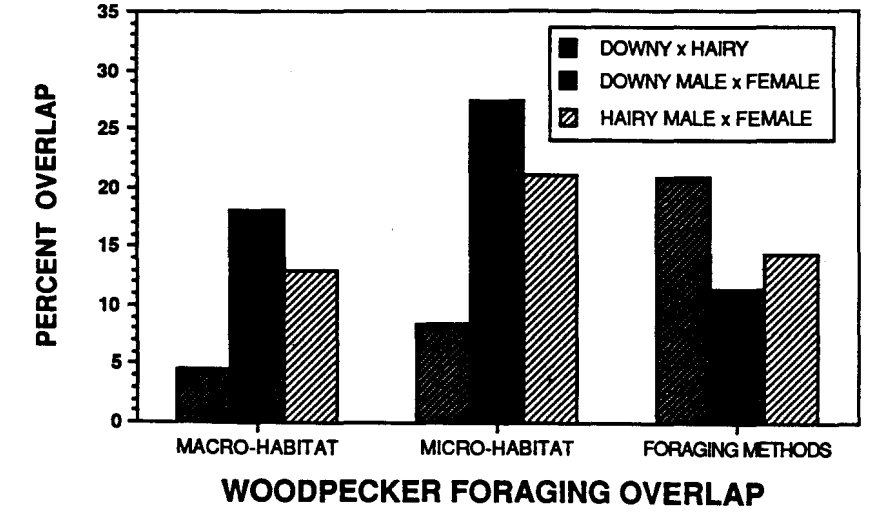


FIGURE 3. *Relative overlap of foraging habitat and methods for female and male Downy and Hairy woodpeckers using percent density overlap (Harner and Whitmore 1977) for foraging macro- and micro-habitat overlap and Horn's R_o (Horn 1966) for overlap of foraging*



Brenner et al. (1992), male Downy Woodpeckers foraged primarily on branches and twigs, whereas females selected trunks and limbs most often. Male Downy and female Hairy woodpeckers tended to forage in the upper two-thirds of trees whereas male Hairy and female Downy woodpeckers foraged primarily in the middle third (Fig. 1b). Both sexes of both species used live trees for foraging more than they used dead trees (Fig. 1c).

Downy Woodpeckers used peer-and-poke and pecking more often than other foraging methods (Fig. 2, page 78). Peer-and-poke foraging does not disturb the foraging substrate, and pecking dislodges minimal bark. Hairy Woodpeckers used foraging methods (pecking, excavating, and scaling) that penetrated or disturbed the foraging substrate to a much greater extent than Downy Woodpeckers (Fig. 2).

Patterns of resource overlap between species and sexes differed among foraging habitats and methods (Fig. 3, page 78). Females and males of each woodpecker species overlapped more in their use of foraging micro- and macro-habitat than the two species overlapped. In contrast, female and male woodpeckers of each species diverged more in their use of foraging methods than did species. Female and male Downy Woodpeckers were more similar in their use of macro- and micro-habitat than female and male Hairy Woodpeckers, but less similar in the selection of foraging methods (Fig. 3).

DISCUSSION

Based on their selection of different foraging micro-habitats and use of different foraging methods (Table 2, Figs. 1 and 2), resource partitioning appears to be well developed among female and male Downy and Hairy woodpeckers. Over their range, however, the generalized foraging patterns used by female and male Hairy and particularly Downy woodpeckers appear to be quite flexible as a function of current competitive pressure (Williams 1980), weather severity (Grubb 1975, 1977; Travis 1977), availability of food (Kilham 1961, 1965, 1970, 1973; Peters and Grubb 1983; Lima 1984), and social interactions (Grubb and Woodrey 1990, Matthysen et al. 1991).

Downy and Hairy woodpeckers appear to be quite opportunistic feeders, and are known to concentrate on insect infestations (Massey and Wygant 1954, Blackford 1955, Yeager 1955, Koplin 1969). Plasticity of foraging behavior would be essential to exploit "blooms" of prey species. Although many observations of foraging patterns in my study are consistent with previous reports, the variety of differences in the foraging patterns of these two species as reported by others reflect the relative plasticity of their foraging behavior (Conner 1981). Unlike my study, Jackson (1970) detected a significant difference between the foraging heights of female and male Downy Woodpeckers. When male Downy Woodpeckers forage on small diameter stems in a mature forest, such stems are usually located relatively high above the ground. Because my study area included agricultural lands, clearcuts, and other areas with low sparse, second growth, male Downy Woodpeckers could find twig size stems closer to the ground than in mature forests. Thus, male Downy Woodpeckers may select foraging sites more on a basis of stem size, and are flexible with respect to height above the ground. Brenner et al. (1992) suggested that Downy Woodpeckers prefer ecotone type habitat but he did not measure the heights of foraging woodpeckers above the ground.

Kisiel (1972) noted that female Hairy Woodpeckers foraged on live trees to a greater extent than did males, and he found no sexual differences in woodpecker foraging heights in New York. I found the opposite in my study, male Hairy Woodpeckers used live trees more frequently than females, and I observed that females foraged higher in trees than males. In Virgina, female and male Downy Woodpeckers showed very little difference in use of live and dead trees as foraging sites. In Kansas, however, differences in Downy Woodpeckers selection of live and dead trees do exist if height of the foraging woodpecker is considered simultaneously (Jackson 1970).

Intra- and interspecific comparisons of foraging resource overlap varied among habitat and behavior categories (Fig. 3). Intraspecific overlap was greater than interspecific overlap when forest stand structure and position of woodpeckers within trees were examined. In contrast, overlap of foraging methods was greater between species than between sexes. This apparent contradiction clarifies if viewed in greater depth. Pairs of woodpeckers often occupy the same territory, particularly during breeding and post-breeding seasons when sexes are often observed foraging together. Thus, a high degree of overlap of foraging macro-habitat between sexes relative to overlap between species is reasonable to expect (Table 1).

Examination of univariate data measured at foraging macro- and micro-habitats suggests that there may be greater differences between sexes' use of micro-habitat than their use of macro-habitat (Tables 1 and 2). Male Hairy and female Downy woodpeckers have very similar use patterns of stem sizes (Fig. 1a) and both also tend to forage in similar vertical positions within trees (Fig. 1b). Male Hairy and female Downy woodpeckers also have the greatest difference in bill sizes (Selander 1965, Willson et al. 1975) and use quite different foraging methods (Fig. 2), possibly permitting a high similarity of foraging site selection with minimal competitive expense.

There was greater overlap between species than between sexes for foraging methods used by the congeneric woodpeckers (Fig. 3). This suggests that past competitive pressures between female and male woodpeckers of both species may have been greater than divergent selective pressures on foraging methods between the two species. Competitive pressures, however, are also affected by overlap in use of forest stand conditions (macro-habitat) and positions selected for foraging within trees (micro-habitat) which confound the ability to focus on the critical overlap between species-sex combinations. Because of differences in the variables and methods used in this study to measure the habitat and behavioral components of species' foraging niches, it is very difficult, if not impossible, to determine which category (macro-habitat, micro-habitat, or foraging methods) is most critical ecologically in partitioning the foraging resources.

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APPENDIX TABLE 1. *Foraging behavior and habitat variables studied*

Macro-foraging habitat (three 11.2-m radius plots at each foraging site)

- Basal area m^2/ha measured with a prism
- Density of stems: number of stems 6 cm diameter per 1/25 ha
- Average height (m) to top of crown canopy measured with a clinometer

Micro-foraging habitat

- Height (m) of foraging woodpecker above the ground (clinometer)
- Diameter of the stem (branch, bole, etc)(cm) where foraging occurred
- Height of the tree (m) in which the woodpecker foraged (clinometer)
- Diameter at breast height (cm) of the tree used for foraging (caliper)
- Standardized height of foraging woodpeckers in the tree (%)

Foraging methods

- Peer-and-poke, a surface gleaning technique
- Pecking on the foraging substrate
- Scaling bark off a tree
- Subcambial excavation at one location for 15 seconds
- Aerial forays to capture insects (hawking)
- Consumption of any vegetable material
- Foraging on the ground