FORAGING BEHAVIOR OF *DENDROCOPOS VILLOSUS* AND *D. PUBESCENS* IN EASTERN NEW YORK STATE

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Studies on differential foraging behavior have usually pertained to the interspecific level (Lack 1947; MacArthur 1958; Dixon 1961; Brewer 1963; Koplin 1969; Koplin and Baldwin 1970). Some recent emphasis, however, has been placed on intraspecific differences (Kilham 1965, 1970; Storer 1966; Selander 1966; Koplin 1967; Ligon 1968; Jackson 1970; Willson 1970). Kilham (1965) noted that female Hairy Woodpeckers (*Dendrocopos villosus*) feed on elms dying of the Dutch elm disease more frequently than males, and he stated that this differential feeding is adaptive by making more effective use of the environment. Concurrent studies by Jackson (1970), Kilham (1970), and Willson (1970) have shown intersexual partitioning of the foraging niche in the Downy Woodpecker (*D. pubescens*). Selander and Giller (1963) found that the degree of sexual dimorphism in culmen length of *Centurus* woodpeckers is greater than any other morphological measurement compared. Their proposal that this disproportionate degree of sexual dimorphism in trophic structure is adaptive and serves to alleviate intersexual competition for food was later confirmed by Selander (1966). In support of this postulate, Koplin (1967) found that the intersexual difference in culmen length of the Northern Three-toed Woodpecker (*Picoides tridactylus*) correlated with spatial, temporal, and dietary differences in the feeding ecology of the sexes. However, he found no significant differences in foraging behavior of either the Hairy or Downy Woodpeckers, probably because the spruce-fir forest is a marginal habitat for both species.

As both the Hairy and Downy Woodpeckers are common residents of the maple-beech-hemlock forests of New York, I undertook this study to determine whether there are spatial or temporal differences in their foraging behavior in this location, which correlate with interspecific and intersexual differences in culmen length.

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METHODS

Observations were made from 1 October 1966, through 18 March 1967. In most cases observations extended from daybreak to midmorning, but occasionally were continued into the afternoon. Both Hairy and Downy Woodpeckers were commonly found in forested areas surrounding ponds or lakes, wooded areas on a flood plain or river bank, and swamp-like locations. For each individual observation I recorded the time of day, the species and sex of the foraging woodpecker, the species and condition of the tree or shrub foraged upon, the position (size of feeding perch) in the tree or shrub, the diameter of the tree or shrub at each position, and the amount of time (measured by a stopwatch) each site was occupied. The general behavior of the woodpecker was recorded, including any conflicts with other woodpeckers of the same or different species.

Feeding technique was divided into two categories: gleaning and drilling. Gleaning behavior is superficial feeding, while drilling is subcambial feeding involving pecking and persistent tapping (Kilham 1965). Feeding positions were classified as trunk, branch, or twig, twig being defined as the terminal portion of a branch less than ¼-in. in diameter.

A Chi-square contingency test was used to evaluate the frequency of occurrence in each of the categories. Only differences $\leqslant 0.05$ level of significance were rejected. The spatial component of foraging behavior was calculated by using a modification of the index to the degree of distinctiveness proposed by Brewer (1963). The summed differences were arbitrarily divided by 200 to achieve an index of difference that ranged from 0.00 at complete overlap through 1.00 at no overlap. Temporal differences were not analyzed statistically because units of time are not independent events (Ligon 1968). Therefore, the index of difference for the temporal component was computed only with the total per cent difference of each category.

RESULTS

SPATIAL DIFFERENCES AT THE INTERSPECIFIC LEVEL

In comparing frequencies of substrate use, I found Hairy Woodpeckers most frequently on aspen (*Populus*) and Downy Woodpeckers on elm (*Ulmus*) (table 1). Although both woodpeckers occurred significantly more often on living than on dead substrata, the per cent difference was not very great (19%). Both species visited the same sites on the foraging substrata. However, Downy Woodpeckers occurred significantly more often on twigs than Hairy Woodpeckers, whereas the latter

TABLE 1. Comparison of foraging occurrences by *D. villosus* and *D. pubescens*.*

No. of occurrences	*D. villosus*			*D. pubescens*		
	Male (82)	Female (46)	Combined (128)	Male (133)	Female (110)	Combined (243)
Tree species						
Aspen	36.6[b]	13.0[b]	28.1[a]	15.0[c]	4.5[c]	10.3[a]
Elm	15.6	23.9	18.8[a]	36.8	40.0	38.3[a]
White Oak	4.9[b]	28.3[b]	13.3	12.0	20.9	16.0
Paper Birch	0.0[b]	19.6[b]	7.0[a]	0.0	0.0	0.0[a]
Shag. Hickory	0.0	2.2	0.8	0.0	0.0	0.0
Stag. Sumac	0.0	0.0	0.0[a]	12.8[c]	0.0[c]	7.0[a]
Pitch Pine	6.1	2.2	4.7	0.0[c]	4.5[c]	2.2
Red Pine	0.0	0.0	0.0[a]	0.0[c]	10.0[c]	4.5[a]
White Pine	7.3	0.0	4.7	1.5[c]	9.1[c]	4.9
Other	29.5	10.8	22.6	21.9	11.0	16.8
Tree condition						
Living	48.8[b]	84.8[b]	61.7[a]	66.2	77.3	71.2[a]
Dead	51.2[b]	15.2[b]	38.3[a]	33.8	22.7	28.8[a]
Foraging site						
Twig	0.0	2.2	0.8[a]	24.1[c]	1.8[c]	14.0[a]
Branch	59.8[b]	43.5[b]	53.9	51.8[c]	34.6[c]	44.0
Trunk	40.2	54.3	45.3	24.1[c]	63.6[c]	42.0
Diameter of foraging site (inches)						
$\leqslant 1$	17.1	10.8	14.9[a]	73.7[c]	17.3[c]	48.1[a]
$>1 \leqslant 2$	23.2	17.4	21.1	14.3	17.3	15.6
$>2 \leqslant 4$	35.4	37.0	35.9[a]	6.0[c]	25.4[c]	14.8[a]
$>4 \leqslant 6$	20.7	19.6	20.3[a]	5.3[c]	20.9[c]	12.4[a]
>6	3.6[b]	15.2[b]	7.8	0.7[c]	19.1[c]	9.1
Foraging technique						
Drilling	76.8	84.8	79.7	79.7[c]	65.4[c]	72.8
Gleaning	23.2	15.2	20.3	20.3[c]	24.6[c]	26.2

* Figures are % of occurrences.
[a] Interspecific difference for that given row ($p \leq 0.05$).
[b] *D. villosus* intersexual differences for that given row ($p \leq 0.05$).
[c] *D. pubescens* intersexual difference for that given row ($p \leq 0.05$). (Discrepancies between figures in the text and those given above are due to rounding in the former.)

tended to occupy branches between 2 and 6 in. in diameter (table 1).

TEMPORAL DIFFERENCES AT THE INTERSPECIFIC LEVEL

Downy Woodpeckers spent most of their foraging time on elm (60%), while Hairy Woodpeckers foraged on aspen (21%) and elm (33%) in approximately equal amounts, and also utilized other species of trees to a greater extent (table 2). Although both species spent approximately the same proportion of foraging time on trunks and also on branches, Downy Woodpeckers spent more time on twigs. Downy Woodpeckers most often occupied substrata with diameters of 1 in. or less, while Hairy Woodpeckers spent most of their foraging time on substrata with diameters between 2 and 4 in. The same feeding techniques were employed by both species, and little difference was observed beyond the tendency of Hairy Woodpeckers to drill more than Downy Woodpeckers (table 2).

SPATIAL DIFFERENCES AT THE INTERSEXUAL LEVEL

The only significant differences in frequency of occurrence on foraging substrata between the sexes of Downy Woodpeckers were that males tended to frequent aspen and staghorn sumac (*Rhus typhina*), while females occurred more on pines (*Pinus rigida*, *P. rugosa*, *P. strobus*). These differences accounted for approximately 25% of the feeding occurrences; most of the foraging occurred on elm and white oak (*Quercus alba*), which were equally frequented by both sexes. Although females showed no preference for any diameter class, they occupied positions on larger foraging sites and trunks significantly more often than did males. Males, on the other hand, foraged more often on branches and twigs, with 74% of the occurrences on sites with diameters of 1 in. or less. Males also foraged more by drilling and less by gleaning than did females (table 1).

TABLE 2. Comparison of foraging time of *D. villosus* and *D. pubescens*.*

Seconds of utilization	*D. villosus*			*D. pubescens*		
	Male (8007)	Female (3953)	Combined (11960)	Male (10518)	Female (9193)	Combined (19711)
Tree species						
Aspen	31.4	11.5	21.4	6.9	2.5	4.7
Elm	23.6	42.7	33.2	61.1	60.0	60.5
White Oak	3.6	12.6	8.1	8.8	17.6	13.2
Paper Birch	0.0	10.1	5.0	0.0	0.0	0.0
Shag. Hickory	0.0	16.0	8.0	0.0	0.0	0.0
Stag. Sumac	0.0	0.0	0.0	2.8	0.0	1.4
Pitch Pine	4.7	2.0	3.3	0.0	4.5	2.2
Red Pine	0.0	0.0	0.0	0.0	5.5	2.8
White Pine	11.2	0.0	5.6	0.2	6.9	3.6
Other	25.5	5.1	15.4	20.2	3.0	11.6
Tree condition						
Living	45.9	75.3	55.6	59.8	71.1	65.0
Dead	54.1	24.7	44.4	40.2	28.9	35.0
Foraging site						
Twig	0.0	1.8	0.6	15.5	0.7	8.5
Branch	60.8	62.5	61.3	70.3	36.8	54.7
Trunk	39.2	35.7	38.1	14.2	62.5	36.8
Diameter of foraging site (inches)						
$\leqslant 1$	12.9	7.6	11.1	70.5	11.8	43.1
$> 1 \leqslant 2$	20.0	22.2	20.7	19.5	16.1	17.9
$> 2 \leqslant 4$	41.0	40.7	40.9	6.1	41.2	22.5
$> 4 \leqslant 6$	24.3	18.6	22.4	3.0	16.2	9.1
> 6	1.8	10.9	4.9	0.9	14.7	7.4
Foraging technique						
Drilling	95.0	91.1	93.7	91.6	73.1	82.9
Gleaning	5.0	8.9	6.3	8.4	26.9	17.1

* Figures are % of seconds of utilization.
(Discrepancies between figures in the text and those given above are due to rounding in the former.)

Hairy Woodpeckers exhibited a greater variability in the frequency of occurrence on foraging substrata. However, significant differences existed in only three cases: males occupied aspen more often than females; females occupied white oak and paper birch (*Betula papyrifera*) more often than males; and females frequented living trees, while males were found more often on dead ones. The only significant differences between the sexes in occupying the various foraging sites and diameter classes were that males occurred more on branches and less on sites greater than 6 in. The difference in feeding technique was not significant, although females tended to drill more and glean less than males (table 1).

TEMPORAL DIFFERENCES AT THE INTERSEXUAL LEVEL

Both sexes of Downy Woodpeckers spent essentially equal amounts of time (60% vs. 61%) foraging on elm, but females utilized white oak twice as often as did males. Males spent 70% of the time on branches and 70% on substrata with diameters of 1 in. or less; females spent 62% of the time on trunks and 42% on substrata with diameters between 2 and 4 in. Males spent 92% of the foraging time drilling, as opposed to only 73% by females (table 2).

Both sexes of Hairy Woodpeckers foraged over half of the time on aspen and elm, with males preferring aspen and females preferring elm. Females fed more on living trees than did males. Both sexes spent approximately equal amounts of time on the various sites and all of the diameter classes, except sites greater than 6 in., which were utilized more by females. Both sexes foraged mainly by drilling (table 2).

AGONISTIC BEHAVIOR

Although I never observed two or more Hairy Woodpeckers feeding on the same tree, I did find Downy Woodpeckers feeding together often. In these cases I witnessed no overt aggressive behavior. Both species fed in mixed

TABLE 3. Summary of differences within the spatial component of the feeding ecology of *D. pubescens* and *D. villosus*.

Foraging behavior	Interspecific index of difference	Intersexual index of difference	
		D. pubescens	*D. villosus*
Substrate preference	0.35	0.27	0.33
Position on foraging substrate	0.07	0.40	0.08
Diameter of foraging substrate	0.31	0.55	0.06
Condition of foraging substrate	0.10	N.S.	0.36
Feeding technique	N.S.	0.14	N.S.
Average difference	0.18	0.29	0.18

(Since values for both position on and diameter of foraging substrate largely measure the same foraging component, the indices calculated for the average difference are biased to some extent. However, the same relative proportions still exist between the columns regardless of which of the two foraging components is excluded.)
N.S. = Not Significant.

TABLE 4. Summary of differences within the temporal component of the feeding ecology of *D. pubescens* and *D. villosus*.

Foraging behavior	Interspecific index of difference	Intersexual index of difference	
		D. pubescens	*D. villosus*
Substrate preference	0.46	0.27	0.56
Position on foraging substrate	0.08	0.48	0.04
Diameter of foraging substrate	0.35	0.62	0.11
Condition of foraging substrate	0.09	0.11	0.29
Feeding technique	0.11	0.19	0.04
Average difference	0.22	0.33	0.21

(Since values for both position on and diameter of foraging substrate largely measure the same foraging component, the indices calculated for the average difference are biased to some extent. However, the same relative proportions still exist between the columns regardless of which of the two foraging components is excluded.)

groups on neighboring trees. These mixed flocks included Black-capped Chickadees (*Parus atricapillus*), Brown Creepers (*Certhia familiaris*), and White-breasted Nuthatches (*Sitta carolinensis*).

There were several conflicts between Hairy and Downy Woodpeckers. In three instances, a Hairy Woodpecker left its foraging site to supplant a Downy Woodpecker. On two of these occasions, the Downy Woodpecker was actively displaced, but returned to its original position as soon as the Hairy Woodpecker left. In the third instance, the Downy Woodpecker was displaced only a few inches while the Hairy Woodpecker completed its brief stay. All three of these cases involved displacement of a male Downy Woodpecker by either sex of the Hairy Woodpecker. Two encounters between a Hairy Woodpecker and a female Downy Woodpecker were seen, but no displacement occurred.

DISCUSSION

In anticipating behavioral differences at the interspecific and intersexual levels, I expected to find the greatest disparity at the interspecific level. Also, as shown by Selander (1966) and Koplin (1967), the degree of difference at the intersexual level should correlate with the degree of sexual dimorphism. The indices of difference in the spatial and temporal components between the sexes of the Hairy Woodpecker are comparable in magnitude to the indices of difference at the interspecific level (tables 3 and 4).

At the interspecific level, the two species of woodpeckers appear to subdivide the feeding resources first, by selecting different species of trees and shrubs, and second, by selecting different locations on the foraging substrata. Hairy Woodpeckers feed on a wide variety of trees and occupy positions on the trunks and larger branches, whereas Downy Woodpeckers feed mostly on elm and occupy positions on small branches and twigs. This more restrictive foraging adaptation of the latter species supports previous findings (Koplin 1969; Jackson 1970; Willson 1970). High indices of difference for both foraging substrate and diameter size also suggest a differential preference in both the spatial and temporal components of feeding behavior between these two species. Although the feeding techniques employed by both species are not significantly different, Hairy Woodpeckers, with their larger and longer bills, are better adapted to feed at the deeper levels in the bark and cambial layers. Thus, they would be expected to forage on trunks and larger branches. The smaller Downy Woodpecker, which is also lighter in weight, digs less deeply and thus is better adapted to feed on terminal branches and twigs by both gleaning and probing.

As there is less morphological difference between the sexes of the Downy Woodpecker than between either the sexes of the Hairy Woodpecker or the two species (Koplin 1967), the least degree of difference in the foraging behavior would be expected between the sexes of the Downy Woodpecker. In contrast to other studies (see Ligon 1968), this was not the case. There was more overall difference

in foraging behavior between the sexes of the Downy Woodpecker than between either the sexes of the Hairy Woodpecker or the two species. Furthermore, because Selander (1966) and Koplin (1967) found that the smaller sexes of *Centurus* spp. and *Picoides tridactylus* foraged upon smaller substrata, I expected to find the smaller sexes of *Dendrocopos* spp. also foraging upon smaller substrata. This was the case for Hairy Woodpeckers, but not for Downy Woodpeckers. The size difference between the sexes of the Downy Woodpecker is statistically insignificant (Koplin 1967) and, therefore, should not be great enough to have an influence on the diameter of and position on substrate selected. Yet, the data in this study show that there is a negative correlation between size of the sexes and size of the foraging substrate. This aspect of their foraging behavior may be a result of their utilization of different feeding techniques. Instead of Downy Woodpeckers foraging upon alternate substrata, selection for differential foraging technique appears to be the result of the similarity in culmen length. Males, feeding on the outer branches and twigs where the bark is thin, tend to drill whereas females, feeding on the trunk and inner, larger branches where the bark would be thicker, tend to glean. Behavioral divergences between sexes which have little morphological differences have also been demonstrated for the Red-cockaded Woodpecker (*Dendrocopos borealis*) (Ligon 1968), for other populations of Downy Woodpeckers (Jackson 1970; Kilham 1970), as well as for the Red-eyed Vireo (*Vireo olivaceus*) (Williamson 1971).

It appears, then, that the selective adaptation to lessen intersexual competition in Downy Woodpeckers has resulted in a behavioral dimorphism in foraging technique rather than in a structural dimorphism of the culmen. In those studies where a statistical difference in culmen length does exist (Willson 1970), both strategies may be operating to subdivide the foraging niche.

Hairy Woodpeckers utilize a generalized foraging pattern where substrate preference is of primary importance in alleviating intersexual competition for food, while condition of and position on the substrate is secondary. A differential foraging technique appears to be of least importance. Downy Woodpeckers exhibit a restricted pattern of intersexual foraging behavior by changing foraging technique and by subdividing the locations on a given foraging substrate.

These overall differences tend to support the speculation of Willson (1970) that intersexual and interspecific differences may often be quite different in alleviating competitive pressures in foraging. Intersexual niche segregation may have resulted in a generalized subdivision of niche dimensions in the dimorphic Hairy Woodpecker, whereas in the monomorphic Downy Woodpecker the result may be a difference in degree of behavioral specialization upon the foraging substratum. Interspecific niche segregation may, however, specifically involve the actual subdivision of the foraging niche dimensions.

If one follows the reasoning of Schoener (1968), the results of the current study suggest that Hairy Woodpeckers may have colonized a relatively "empty niche," thus allowing structural dimorphism and the concurrent (or subsequent) subdivision of the foraging niche. In contrast, Downy Woodpeckers may have colonized a "narrow niche" containing sufficient interspecific competitive pressures to prevent any great sexual dimorphism. In support of this suggestion is the observation that the only other large birds seen in the study area whose foraging habits are similar to those of the Hairy Woodpecker were occasional Yellow-shafted Flickers (*Colaptes auratus*) and Pileated Woodpeckers (*Dryocopus pileatus*). But in locations where Downy Woodpeckers foraged, there were groups of Black-capped Chickadees, Brown Creepers, and White-breasted Nuthatches in constant close proximity.

SUMMARY

Riparian vegetation of the beech-maple-hemlock forests of eastern New York is typical of the foraging habitat for mixed species groups of Downy and Hairy Woodpeckers. Primary mechanisms used in avoiding interspecific competition involve subdivision of the foraging niche by the selection of different trees and shrubs and by the selection of sites on the foraging substrata of different diameter sizes.

Hairy Woodpeckers, with their morphological differences, avoid intersexual competition by foraging on a wide variety of different species of trees with a differential selection of living or dead trees. A minor effect of this selective pressure is a change in feeding technique to include more gleaning by the females.

Downy Woodpeckers, because of their similarity, avoid intersexual competition behaviorally by utilizing differential techniques of feeding on different diameter sizes of the foraging substrate, and on different but fewer species of trees and shrubs.

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