

# SEASONAL FORAGING IN A DOWNY WOODPECKER POPULATION

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Many workers have investigated the response of avian populations to the varying availability and distribution of food in both time (Kilham 1970, Jackson 1970, Willson 1970) and space (MacLellan 1959, Royama 1970). This study investigates the response of a Downy Woodpecker (*Picoides pubescens*) population to the interaction of these two types of heterogeneity. This species forages on the surface of trees (Bent 1939, MacLellan 1959, Lawrence 1967, Jackson 1970, Kisiel 1972, Williams 1975). Eastern mixed forests have tree species of widely differing surface textures and thus of potentially different suitability for harboring food items; I consider this as spatial heterogeneity. I consider the change from summer to winter in food availability as temporal patchiness. I use spatial movement patterns and substrate choice, two aspects of foraging behavior, as the variables against which to assess the response of the population to this compound heterogeneity.

## METHODS

The study was conducted along two high, steep streambanks in a mesophytic forest near the Morris Arboretum, Philadelphia, Pennsylvania. The canopy trees were chiefly American Beech (*Fagus grandifolia*), Sweet Birch (*Betula lenta*), Tulip-tree (*Liriodendron tulipifera*), Boxelder (*Acer negundo*), White Oak (*Quercus alba*), Chestnut Oak (*Q. prinus*), Northern Red Oak (*Q. rubra*), and Black Oak (*Q. velutina*); the understory was predominantly Red Maple (*Acer rubrum*) and Flowering Dogwood (*Cornus florida*). The relative proportions of constituent trees were estimated in two ways. First, all trees with trunks greater than 5 cm dbh and growing within six circles with a combined area of 0.18 hectares were counted and identified to species; second, information collected by D. Sprugel in 1974 was consulted.

The birds were studied during July, August, and December 1974 and January 1975 by walking along foot paths through the forest and noting the location of all individuals observed as well as flight directions and aggressive intraspecific interactions. Non-foraging individuals were noted for census purposes only. Data taken for each foraging observation were sex of bird, species of tree used, diameter of tree, use of trunk or limbs, foraging height, and range of foraging height (in the cases of continuous movement along a bole or within a group of limbs). I was not able to consistently time my observations, so each datum is one discrete observation.

The unit for studying spatial movement patterns is a foraging bout, defined here as an observed progression of uninterrupted foraging on at least four consecutive trees. A foraging bird was followed visually as it moved from tree to tree until it could

no longer be seen. Any displacements or other interruptions were considered to terminate a bout. Bouts ranged from four to eight trees in duration, and the data listed above were taken for each tree visited in a bout. As the birds flew directly from tree to tree, measuring the distances between trees and the angles between successive flights provided an accurate description of the pattern of movement.

I left an area after each bout to avoid bias toward a particular bird. Distances were measured by pacing and angles by triangulation or compass. Observations were made under weather conditions from clear skies to snowfall on both calm and windy days.

As foraging substrates were trees of either smooth or rough bark, a method was devised to quantify bark furrowedness. Square cardboard plates (25.4 cm on a side) were randomly pierced with 25 pinholes. A plate was positioned on a tree at breast height and bent so that it touched the bark at all points. Straight wire probes were inserted through the holes, and depth of penetration was measured on a unit scale of 1 unit = 2.5 mm, the smallest unit yielding reproducible results. One plate was used per tree, and 10 trees were measured for each of the five chief genera used as foraging substrates (*Fagus*, *Betula*, *Acer*, *Quercus*, *Liriodendron*). All species initially were treated as distinct. Oaks later were grouped because these species differed little in bark furrowedness and they were infrequent in the study area. Measurements of bark furrowedness were kept in the original units in order to minimize the propagation of error (Ku 1969).

Locations of observations, including those of several intraspecific conflicts, enabled me to delineate a feeding range for each of 4 pairs of Downy Woodpeckers in the summer and 4-5 pairs in the winter. The use of winter feeding ranges parallels the behavior observed by Bent (1939) and Lawrence (1967). Incomplete observations were discarded, save for those lacking only determination of sex (approximately half of all otherwise usable observations); discarding the latter would unduly bias the data against foraging observations that were very high in the canopy.

## RESULTS

### SPATIAL MOVEMENT

The first component of spatial movement is angular orientation, the tendency of a bird to move in a certain direction reflecting, presumably, a preferred foraging path. Each direction of flight from a tree can be measured as an angle from the previous direction of approach. The simplest null hypothesis is one of uniform circular motion in which the new direction has no consistent orientation. Under this hypothesis the expected distribution of "new direction angles" is uniform on 0 to 360 degrees and indicates random turning (Batschelet 1965). The observed angles do

TABLE 1. Foraging substrate choice by Downy Woodpeckers<sup>a</sup>.

Tree species	<i>Fagus</i>		<i>Betula</i>		<i>Quercus</i>		<i>A. negundo</i>		<i>Liriodendron</i>						
Relative frequency in habitat of use by birds	.67	.57	.06	.14	.19	.08	.05	.06	.14	.05	.07	.21	.07	.11	.49
Diameter of tree (m)															
$\bar{x}$	.30	.44	.29	.33	.23	.52	.18	.22	.49	.60					
$S_x$	.19	.15	.17	.10	.25	.13	.20	.14	.04	.13					
Foraging height (m)															
$\bar{x}$	6.09	10.44	6.32	8.74	7.47	10.52	3.76	4.36	12.50	12.19					
$S_x$	3.70	7.42	4.48	3.72	8.05	5.36	3.08	2.62	0.68	4.31					
Number of observations	45	4	9	6	3	9	3	13	5	31					
Bark furrowedness <sup>b</sup>															
$\bar{x}$		1.43		1.74		4.32		3.72		4.34					
$S_x$		.08		.15		.33		.21		.16					

<sup>a</sup> Summer data are in left-hand, winter data in right-hand columns. Center columns indicate constant tree characteristics.

<sup>b</sup> See text for explanation of units.

not reject this hypothesis either in summer ( $\chi^2_3 = 2.34$ ,  $.50 \leq P \leq .75$ ) or in winter ( $\chi^2_3 = 4.33$ ,  $.10 \leq P \leq .25$ ).

Step length, the distance a bird travels from one foraged tree to the next, is the second component of spatial movement. No significant serial correlation of step length sequence was found either in summer ( $r_{21} = .39$ ,  $.05 \leq P \leq .10$ ) or in winter ( $r_{19} = .36$ ,  $.10 \leq P \leq .20$ ), and average step length does not change seasonally ( $\bar{x}_{\text{summer}} = 8.40 \pm 1.13$  m,  $\bar{x}_{\text{winter}} = 10.52 \pm 1.19$  m,  $t_{44} = -1.28$ ,  $.10 \leq P \leq .25$ ).

Thus my findings do not suggest anything other than random movement by the birds.

#### SUBSTRATE USAGE

Table 1 summarizes the data on foraging substrate for summer and winter. The tree proportions include live trees only. I observed foraging on a dead tree only once, although about 4% of all standing trunks in each territory were dead. This contrasts with Willson's (1970) study in which one sex of *P. pubescens* actively preferred dead trees or limbs.

If no substrate preferences exist, then the proportional use of tree species by the birds should match the trees' proportional occurrence in the habitat. Multiplying the total number of foraging observations by the rela-

tive proportions of specific trees in the habitat will generate expected frequencies of trees used which can be compared with the observed frequencies. To ensure the validity of the test, *Quercus* spp. and *A. negundo* were combined so that the expected frequencies in all cells would be greater than six. The results suggest no preference in summer ( $\chi^2_3 = 3.98$ ,  $.25 \leq P \leq .50$ ) but decided specialization in winter ( $\chi^2_3 = 138.20$ ,  $P \leq .001$ ). All observations not made singly or as the first in a bout were then eliminated to allow for any statistical dependence of successive observations. A contingency test on this reduced data set indicated that the winter result was not an artifact ( $\chi^2_1 = 49.34$ ,  $P \leq .001$ ). In winter the birds prefer to forage on *Liriodendron*, *A. negundo*, and *Quercus*, excluding *Betula* and *Fagus* (Table 1).

Table 1 also presents mean bark furrowedness which was tested via the single classification ANOVA shown in Table 2. As significant differences were found, a Newman-Kuels procedure was used to examine where the significance lay. The results in terms of species' means were *Liriodendron* = *Quercus* > *A. negundo* > *Betula* > *Fagus*. Tree species may be ranked as to frequency of woodpecker usage and as to bark furrowedness via these results (note that *Liriodendron* and *Quercus* must be tied in bark furrowedness). Relative frequency of usage and bark furrowedness

TABLE 2. Bark furrowedness: analysis of variance.

Source	Deg. of Freedom	Sum of Squares	Mean Square	F	P	Coeff. of Determ.
Tree species	4	2005.82	501.45	189.05	.0001	.38
Residual	1245	3302.30	2.65			
TOTAL	1249	5308.12				

TABLE 3. Trunk and limb usage by Downy Woodpeckers.

	N	Summer Rel. Freq.	N	Winter Rel. Freq.
Trunks only	31	.50	30	.54
Trunks and branches	5	.08	14 <sup>a</sup>	.25
Branches only	26 <sup>b</sup>	.42	12 <sup>c</sup>	.21

<sup>a</sup> Includes 1 dead limb.  
<sup>b</sup> Includes 2 dead limbs.  
<sup>c</sup> Includes 3 dead limbs.

are significantly correlated (Spearman rank correlation  $r_s = .92$ ,  $P \leq .05$ ) in winter but not in summer ( $r_s = -.68$ ). Relative usage in summer is perfectly correlated with relative abundance rank.

#### FORAGING SITES

Use of trunks and limbs differs in the two seasons, bimodal usage in summer trending toward unimodal usage in the winter (Table 3). A binomial model test shows no significant differences between seasons in the likelihood of trunk use ( $z = -1.34$ ,  $.05 \leq P \leq .10$ ).

Table 4 presents the results of a two-way ANOVA on the size of trees selected for foraging. The significant effect of tree species presumably reflects the intrinsic differences in tree species' size distributions. The significant effect of season shows that, on average, birds foraged on larger trees in the winter. The lack of significant interaction suggests that the seasonal difference is simply the result of intrinsic substrate differences coupled with differential substrate usage in winter (the changing weights due to sample size on each species' mean).

Table 5 presents the results of a two-way ANACOVA on foraging height with size of the tree as covariate; no significant difference emerges. A naive test, simple ANOVA in this case, would have revealed significant differences in foraging height by season; allowing for the size of the tree, these differences vanish, suggesting in conjunction with the results of Table 4 that the species of foraging substrate is the important variable.

TABLE 4. Tree size: analysis of variance.

Source	Deg. of Freedom	Sum of Squares	Mean Square	F	P	Coeff. of Determ.
Season	1	364.85	364.85	9.13	.0034	.06
Tree species	4	1300.40	325.10	8.14	.0001	.20
Season $\times$ sp.	4	169.88	42.47	1.06	NS	
Residual	118	4715.28	39.96			
TOTAL	127	6550.41				

## DISCUSSION

### ROUGH-BARKED TREES

The rough-barked surfaces of trees are important places for insect larvae and pupae to overwinter (MacLellan 1959), and the significance of bark crevices as food sources for the Downy Woodpecker has been discussed by Jackson (1970). In the summer, invertebrates continually reappear on the surfaces of all trees. Smooth-barked trees provide little to no protective or supportive substrate for overwintering invertebrates, while furrowed or flaky barks do. Thus with the change of season, invertebrate food can be harvested only from a restricted subset of bark surfaces; this is the basis for the observed specialization.

Bark furrowedness, however, decreases upward along the trunk. If it does so at the same rate for all types of trees, then the value at breast height is conservative, and the birds may discriminate on the basis of much finer differences. If, as is more likely, the rates are not the same, then woodpeckers may be using other clues beside furrowedness.

Other quantitative assays of Downy Woodpecker foraging have revealed significant specializations on kinds of trees. Kilham (1970) discovered a preference for Paper Birch (*Betula papyrifera*), and Williams (1975) for *Quercus* spp. Both Willson (1970) and Jackson (1970) found birds foraging on trees in quite different proportions from those in which the trees occurred. In Kilham's study the birds were concentrating on likely sources of a coccid beetle; Jackson interpreted his results to indicate a likelihood of finding food, and my study suggests a similar phenomenon. In Willson's and Jackson's winter data, the preferred trees have rough bark.

### FORAGING SITES

The tendency toward less usage of branches in winter could reflect the same biological factor as that prompting the preference for certain trees. Branches are not furrowed in the manner of a trunk, and in winter they

TABLE 5. Foraging height: analysis of covariance.

Source	Deg. of Freedom	Sum of Squares	Mean Square	F	P
Season	1	43.42	43.42	.299	.59
Tree species	4	1004.16	251.02	1.7276	.15
Season × sp.	4	463.72	115.93	.7978	.53
Residual	117	17001.27	145.31		
TOTAL	126	18512.56			

may be poor sources of food (see Jackson 1970).

The ANACOVA suggests that foraging height is proportional to size of tree; a similar result was found by Jackson (1970) for foraging height and tree height. When one accounts for this relation, no seasonal change occurs in foraging height, in marked contrast to the results of Grubb (1975). Grubb found Downy Woodpeckers to forage lower, increasing their use of trunks and large branches on cold days in winter, presumably to minimize chilling due to wind and ambient temperature.

I suggest that these responses may also make it easier to find food because the areas of lessened thermal stress for the birds are also the most favorable for invertebrates. The lack of seasonal difference in foraging height suggests one or more of the following: data are insufficient to reveal weather effects; on average, the weather conditions were never sufficiently stressful to prompt a change in the birds' regular pattern; weather conditions also affect the size or the species of trees selected for foraging.

#### PATCH RECOGNITION

The MacArthur-Pianka (1966) model predicts that with increased differences in patch quality an organism should become more specialized in the number of patch types used in order to continue an "optimal utilization" of a heterogeneous habitat. This model is useful only if a patch unit can be identified. In the present case, winter conditions increase the differences in the suitability of various species of trees for foraging. The birds respond by specializing on rarer species, yet maintaining random motion. Disregarding failure of the analysis, this could occur in two ways. Either all trees are randomly distributed, or tree species occur in a mosaic of clumps. In the former case the patch unit is an individual tree; in the latter, a monotypic clump.

Vegetation studies (Williamson 1975) suggest that the latter case is closer to reality. If so, then the model can be used to explain

the birds' behavior of concentrating their foraging in a clump of trees with suitable substrates. This is supported by qualitative observations on the site. *Liriodendron* tends to occur with *A. negundo* along the streambank at the bottom of the slope, and with *Quercus* spp. atop the ridges. *Betula* occurs along the lower slopes interspersed with *Fagus*, while *Fagus* continues up the hillside as the dominant species. Further, if the hypothesis of random dispersion were true, the average step length would have to increase in winter because, given the observed proportions of trees, a bird would have to travel further on average in order to concentrate on rarer tree species. The data refute this. Two predictions arise: (1) in this population no viable year-round feeding range can contain solely *Fagus* and *Betula*; (2) directed movement must be present but on a larger scale than could be detected in this study.

An analogous process can be used to interpret the weather-dependent habitat use found by Grubb (1977). In his case, topographic patterns produced "patches" of varying thermal suitability in winter. As weather worsened (increased differences in patch quality), Downy Woodpeckers restricted their foraging to those patches most sheltered from adverse conditions. I did not consider this variety of heterogeneity in my study.

The behavioral ability to respond to patchiness appears to exist in tits (Paridae, Royama 1970) as well as Downy Woodpeckers (Knight 1958). MacLellan (1959) found concentrations of feeding Downy Woodpeckers throughout a territory and found insect larvae and other invertebrate resources to be more abundant in these patches. Experimental evidence suggests that tits can recognize temporal fluctuations in patch quality (Smith and Sweatman 1974), and my field observations predict that Downy Woodpeckers should possess a similar faculty.

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