FORAGING BEHAVIOR OF SOME WINTER BIRDS OF DECIDUOUS WOODS

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Niche segregation among members of a community has attracted considerable attention from many ecologists in the past few decades. The discovery and enumeration of interspecific differences in various niche dimensions is a popular exercise, yet all too often work ceases with a simple list of differences between more or less similar, coexisting species. More general treatments are relatively rare (but see, e.g., Cody 1968) and yet are essential if we are to understand the basis of community composition and organization and if we are to relate field and laboratory information to the more theoretical discussions presented by Hutchinson and MacArthur (1959), Schoener (1965), Selander (1966), and others.

Of special import are comparative studies of different communities (a variety of habitats, taxonomic groupings, trophic levels, etc.) with respect to the magnitudes and kinds of differences among distinct phenotypic categories, be they species, sexes, or whatever, and to the variation within each phenotypic category. With quantities of these kinds of data in hand, it may then be possible to approach with empirical models the question of the regulation of species (and phenotypic) diversity.

The present paper is the first of a projected series dealing with problems of comparative niche segregation and variations in avian species diversity. Since the paper deals only with one woodland, comparative aspects are limited to a consideration of intersexual differences in foraging behavior.

STUDY AREA AND METHODS

Brownfield Woods, near Champaign-Urbana, is a woodlot of about 60 acres, surrounded on all sides by cultivated fields and houses. Vegetation was sampled by the point-quarter method on several transects through the woods, 95 points comprising the total sample. The principal trees are sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and hackberry (*Celtis occidentalis*). Other large trees present in some abundance include *Quercus macrocarpa* and *Q. muhlenbergii* (bur and chinquapin oaks), *Fraxinus americana* (white ash), *Ulmus americana* and *U. rubra* (American and slippery elms), *Carya* spp. (mainly *ovata*, shagbark hickory), *Tilia americana* (basswood), *Juglans nigra* (walnut), and *Aesculus glabra* (buckeye). A well developed understory is composed primarily of maple saplings, spice bush (*Lindera benzoin*) and pawpaw (*Asimina triloba*). A luxuriant ground cover features mainly *Hydrophyllum* spp. and stinging wood nettle (*Laportea canadensis*), with an abundance of fallen trees and branches. A small stream, full only after a rain or thaw, courses through the area.

Observations were made in winter (mid-November–late March) and spring (late March–late June) of 1966–1967; almost no woodpeckers inhabited the woods the next winter. Foraging data were obtained while censusing the woods, cruising slowly along a marked grid system, stopping frequently. No effort was made to follow individual birds for long periods of time. The data for the tiny and inconspicuous Brown Creeper may be slightly biased toward lower heights, although special searches were made for this species higher in the trees in an effort to compensate for the difficulty of seeing the birds high in the canopy.

RESULTS

Foraging behavior of several wintering species is presented in tables 1–4. Chi-square tests for differences between bird species and sexes and between seasons were made using only pairs of cells containing non-zero entries. Addition of data in paired comparisons in which one sample yields some "zero" entries, while not testable with χ^2, should only increase the biological significance of tested differences. The tests were, of course, performed on the original, numerical data, not on the more easily read frequencies presented in the tables.

Virtually all the phenotypes differed in their utilization of the foraging space and showed seasonal variation in the exploitation patterns (table 1). All comparisons between morphs and between seasons showed a significant difference ($P < 0.05$) except male Red-bellied Woodpecker (*Centurus carolinus*) vs. White-breasted Nuthatch (*Sitta carolinensis*), and female red-belly vs. female Downy Woodpecker (*Dendrocopos pubescens*) in winter. In the latter case, a glance at the table shows plainly that the insignificance of the tested difference is probably due to the large number of cells containing zeroes for the female red-belly, which necessitated ignoring many data entries for the female downy. I am sure that

TABLE 1. Utilization (per cent of observation time) of different types of trees.

Tree types and relative frequencies	White-breasted Nuthatch	Brown Creeper		Red-headed Woodpecker		♂Red-bellied Woodpecker		♀Red-bellied Woodpecker		♂Downy Woodpecker		♀Downy Woodpecker	
	winter	winter	spring	winter	spring	winter	spring	winter	spring	winter	spring	winter	spring
oaks (15%)	56	51	8	31	32	58	11	58	29	40	17	28	19
maple (55%)	8	24	14	39	32	9	31	42	41	26	56	20	41
ash (5%)	34	3	6	14	+	31	29	−	9	−	−	7	5
hackberry (6%)	2	13	30	3	5	2	13	−	−	3	−	28	−
elms (4%)	−	8	19	6	5	−	11	−	−	22	9	12	−
hickories (+)	−	−	−	1	4	−	−	−	−	−	−	1	31
basswood (4%)	−	−	10	4	+	−	−	−	−	−	−	1	−
walnut (2%)	−	1	9	1	+	−	2	−	−	−	−	2	4
dead (7%)	−	−	4	1	21	−	3	−	21	9	+	1	−
buckeye (1%)	−	−	−	−	−	−	−	−	−	−	18	−	−
Observation (sec)	930	8942	2479	5919	4965	3156	2829	1793	1348	1670	822	6663	2218

the biological importance of the statistically insignificant difference in tree utilization is real.

All phenotypic classes preferred oaks in the winter, two also concentrated on maple or hackberry, and most switched to maple as the primary tree in spring, the most notable exception being the Brown Creeper (*Certhia familiaris*), which then preferred hackberry. Secondary choices manifested considerably more variation.

Distribution of feeding activity among the various types of trees differed ($P < 0.05$) in all phenotypes from the estimated frequencies of tree types in the woods (based on trees of > 6 inches D.B.H.), indicating that all forms were more or less selective in their choice of tree. Several species, notably the woodpeckers, frequently foraged in the nearby cornfields, but this behavior could not be timed since the birds were usually out of sight.

Most of the phenotypic classes used some special foraging techniques (see table 2), and usually differed from each other in their frequency of using these methods.

Preferred "feeding sites" were highly varied and had a much smaller (but still significant)

TABLE 2. Per cent of time spent in special foraging techniques[a].

	Tapping and hammering		Flaking (a sideways blow)	
	winter	spring	winter	spring
♂ Red-bellied Woodpecker	2	5	−	−
Red-headed Woodpecker	13	14	−	−
♀ Downy Woodpecker	22	15	4	−
♂ Downy Woodpecker	22	−	−	−
White-breasted Nuthatch	7	−	1	−

[a] All comparisons between phenotypes and seasons differ significantly ($P < 0.05$) except ♂ vs. ♀ Downy Woodpeckers in winter, using χ^2 on original data.

seasonal shift (table 3). All phenotypes differed significantly ($P < 0.05$) from each other. In winter the White-breasted Nuthatch and Red-bellied Woodpeckers used large live branches especially; Brown Creepers and female Downy Woodpeckers selected primarily trunks; Red-headed Woodpeckers (*Melanerpes erythrocephalus*) concentrated on large dead branches; and male downies used a diversity of sites more or less equally. Most of these preferences were continued into spring, with a few additions; data for red-bellies here permitted a distinction between the choices made by male and female: the male selected trunks and large, live branches, the female live branches, both small and large.

Vertical distribution of foraging in winter found both male and female downies in the low ranges, Brown Creepers and nuthatches in the low and middle heights, and red-bellies and red-heads in the upper story of the woods (table 4). The major seasonal shifts were shown by male downies, which moved a major portion of their foraging effort to the canopy; female downies made a minor shift in this direction. Seasonal shifts and comparisons between phenotypic categories are all significant ($P < 0.05$, Kolmogorov-Smirnov two-sample test).

Tendencies to specialize to particular tree species, heights, etc. may be assessed by means of the information theory index

$$H' = -\sum_{i=1}^{s} p_i \log p_i,$$ in which each p_i represents

the proportion of individuals to be found in category i. H' reaches a maximum value for a given s when all p_i's are equal; i.e., when individuals do not tend to concentrate in just a few categories. Thus $J' = H'/H'_{max}$ may be used as an indication of specialization to a few cate-

TABLE 3. Exploitation (per cent of time) of different feeding sites.

Feeding sites diameter (inches)	White-breasted Nuthatch	Brown Creeper		Red-headed Woodpecker		Red-bellied Woodpecker			♂ Downy Woodpecker		♀ Downy Woodpecker	
	winter	winter	spring	winter	spring	winter	spring		winter	spring	winter	spring
							♂	♀				
small trunk (< 6)	3	6	24	3	8	5	2	1	12	24	9	8
medium trunk (6–36)	22	65	66	21	19	12	38	18	12	1	60	31
large trunk (> 36)	5	11	1	4	–	2	–	–	1	–	1	–
live large branch (> 3)	38	9	–	17	21	52	41	32	4	12	10	12
dead large branch (> 3)	5	4	5	32	28	15	17	9	15	8	3	7
live small branch (< 3)	21	1	–	12	9	8	–	30	29	28	9	19
dead small branch (< 3)	–	–	–	6	1	1	–	–	22	26	1	4
broken trunk	2	1	4	5	7	5	2	10	4	1	3	–
vine	–	2	–	–	–	–	–	–	1	–	–	–
log	4	1	–	–	–	–	–	–	1	–	3	19
ground	–	–	–	–	2	–	–	–	–	–	–	–
Observation (sec)	3334	13,643	2484	12,233	5222	9459	2816	1368	5298	1134	8641	3800

gories, a small value of J' representing a relatively strong tendency to specialize (see, e.g., Pielou 1966). In order to facilitate comparisons, the J' values here are calculated using the total possible number of categories available $(i = s)$, not merely the actual number used by each species.

Table 5 lists specialization indices (J') for the several phenotypes. No regular seasonal trends in specialization to tree type, feeding site, or height were apparent, suggesting, perhaps, that neither the influx of spring migrants nor the distribution of spring foods changes the degree of specialization of these birds (or that their effects cancel each other).

In winter the greatest specialist to tree type was the female red-belly, followed by the male of that species and the nuthatch. In spring, the lowest J' values occurred for downies and for female red-bellies. The Brown Creeper was the most specialized to feeding site in both seasons, followed in winter by female downies and the Red-bellied Woodpecker, and in spring by red-bellies and male downies. The

TABLE 4. Vertical distribution (per cent of time) of foraging activity.

Height (ft)	White-breasted Nuthatch	Brown Creeper		Red-headed Woodpecker		Red-bellied Woodpecker			♂ Downy Woodpecker		♀ Downy Woodpecker	
	winter	winter	spring	winter	spring	winter	spring		winter	spring	winter	spring
							♂	♀				
0– 5	3	5	5	2	3	4	1	–	12	15	6	24
5– 10	3	7	16	1	+	1	1	–	24	9	4	9
10– 20	11	17	20	1	3	2	5	12	13	18	25	15
20– 30	19	25	23	4	9	4	6	10	14	9	25	17
30– 40	9	20	10	3	+	4	8	14	18	9	20	6
40– 50	13	14	6	14	4	8	7	7	7	+	8	6
50– 60	13	5	1	11	17	10	12	3	1	+	6	9
60– 70	8	1	1	31	12	20	39	13	3	–	1	–
70– 80	9	3	–	18	27	17	11	23	1	37	3	14
80– 90	9	2	–	10	19	10	5	11	2	–	2	–
90–100	3	1	–	3	5	19	–	7	6	–	–	–
> 100	–	–	–	1	+	1	5	–	–	–	–	–
Observation (sec)	3334	13,643	2484	12,233	5222	9459	2829	1368	5298	1134	8641	3800

TABLE 5. Indices of specialization to foraging place: $J' = H'/H'_{max}$.[a]

	Tree type ($s = 10$)		Feeding site ($s = 11$)		Height ($s = 12$)	
	winter	spring	winter	spring	winter	spring
♂ Red-bellied Woodpecker	0.422	0.699		0.489		0.789
			} 0.623		} 0.853	
♀ Red-bellied Woodpecker	0.296	0.544		0.641		0.839
White-breasted Nuthatch	0.414	–	0.681	–	0.908	–
♂ Downy Woodpecker	0.582	0.515	0.754	0.652	0.822	0.681
♀ Downy Woodpecker	0.722	0.578	0.588	0.738	0.782	0.801
Red-headed Woodpecker	0.664	0.667	0.751	0.738	0.799	0.805
Brown Creeper	0.563	0.827	0.518	0.400	0.804	0.694

[a] See text for full explanation of notation.

Brown Creeper and male downies, relative to the other forms, showed some limitation of foraging height in spring.

In contrast to such specialization, the Red-headed Woodpecker regularly ranked close to the top of the list as a generalist (J' values consistently rather high). This *may* have resulted from the lumping of observations of the indistinguishable males and females (but see below). In addition to the foraging behavior presented in the tables, this species sometimes hawked insects in flight, fed on the ground, and occasionally hovered at oak flowers. These observations were not quantified. Other phenotypes were relatively general foragers at times. The female downy exploited a wide variety of tree types in winter, while, in contrast, the male downy used a diversity of feeding sites (as the female did in spring). Brown Creepers used a variety of tree types in spring, and nuthatches exploited a diversity of heights in winter.

From table 6 it can be seen that the average time spent in each foraging place varied noticeably between phenotypic categories. In general, the nuthatches and male downies moved (flew) from place to place rather quickly, while female red-bellies and Brown Creepers tended to spend considerable time at one site. The figures are somewhat misleading, however, for while the creepers tended to spend a long time on each tree trunk,

TABLE 6. Average time (sec) spent at each feeding place between flights (number of observations in parentheses).

	winter		spring	
Brown Creeper	82	(167)	75	(33)
Red-headed Woodpecker	74	(166)	68	(77)
♂ Downy Woodpecker	36	(147)	38	(30)
♀ Downy Woodpecker	64	(135)	83	(46)
♂ Red-bellied Woodpecker	95	(32)	101	(28)
♀ Red-bellied Woodpecker	46	(24)	72	(19)
White-breasted Nuthatch	26	(130)		

they certainly did not stay in one spot on the trunk, but rather moved almost continuously. This was sometimes also true of the woodpeckers, but to a markedly lesser degree. All species foraged from time to time on the underside of branches in an upside-down position, but only the nuthatch frequently hunted in a head-down position on a vertical surface. All the woodpeckers occasionally and rather awkwardly backed down a branch, the agile nuthatch changed course by turning around and moving head-first, and the creeper almost invariably moved forward and upward. I assume that different kinds and rates of movement tend to expose the predators to somewhat different prey, or at least to prey in different sorts of places, but the small local populations preclude shooting of specimens for gut analyses.

Bill measurements of all species are given in table 7. Downies, red-heads, and red-bellies are all sexually dimorphic in at least one bill dimension; creepers and nuthatches are not. It would have been interesting to compare magnitudes of difference in foraging behavior with the degree of sexual dimorphism in bill dimensions, but unfortunately sexes of red-heads, creepers and nuthatches cannot be distinguished in the field.

Hutchinson (1959) has estimated an average character difference of 1.3 (in the size of the trophic apparatus) between closely related coexisting species. Although none of the members of the scansorial "guild" (Root 1967) considered in this paper belong to the same genus according to most taxonomists, and in fact belong to three different families, the active interspecific aggression between many of them and certain similarities in their hunting habits suggest that competition may be present (despite the statistically significant differences in several aspects of foraging behavior). It may therefore be profitable to look at character differences (CD) in this group.

TABLE 7. Bill dimensions[a] in mm.

Species	Sex	n	Length	Depth	Width	Season
Downy Woodpecker	♂	14	15.7[b]	5.1	4.9	winter
	♀	15	14.9[b]	5.0	4.9	
Downy Woodpecker	♂	10	15.6	5.3[b]	4.9	summer
	♀	10	15.3	4.9[b]	4.7	
Red-headed Woodpecker	♂	14	25.3	7.6[b]	7.8[b]	summer
	♀	16	24.5	7.3[b]	7.5[b]	
Red-bellied Woodpecker	♂	12	27.7[b]	7.5[b]	7.5[b]	winter
	♀	12	25.8[b]	7.0[b]	6.9[b]	
Brown Creeper	♂ & ♀	19	12.8	2.4	1.8	mainly winter
White-breasted Nuthatch	♂ & ♀	29	15.4	3.8	3.9	—

[a] All specimens collected in midwestern states.
[b] Significant difference between sexes in means of the indicated dimension; t-test, $P < 0.05$.

By constructing ratios of large : small for each bill dimension, we may compare the magnitude of conspecific intersexual differences with the degree of interspecific difference. Using only the species and dimensions showing sexual dimorphism, the mean character difference between sexes is 1.06 (range, 1.04–1.09). In contrast, most interspecific differences are much greater: the mean CD (mean of all three bill dimensions and all interspecific paired comparisons) for Brown Creeper, nuthatch, winter downies, red-heads, and red-bellies are 2.40, 1.62, 1.58, 1.88, and 1.86, respectively. The smallest CDs are found when comparing bill lengths of the creeper, nuthatch, and downy (male and female together), and when comparing all dimensions of red-head and red-belly bills. These CD values are less than 1.20.

In most cases, then, the magnitude of interspecific character difference exceeds the average estimated by Hutchinson, and, in fact, many of them exceed even his extreme values. Since these birds do belong to several families and genera, and hence presumably have very different genetic backgrounds and quite different body plans, perhaps this is not surprising. However, it should not be taken to mean that competition is negligible between species of different taxa.

The very small differences between sexes may find explanation in several possibilities which are discussed later. The size of the CD, however, does not permit a prediction of the amount of overlap (Horn 1966), the form of competition, or the way in which competition may be reduced. Male and female red-bellies sometimes hold at least partially exclusive areas in winter (Stickel 1965; pers. obs.), and red-heads may do the same, but downy males and females are frequently found foraging close together with no sign of spatial segrega-

tion except that associated with different hunting techniques. Red-heads and red-bellies also show little character difference between them (1.06) and generally more overlap in foraging than the sexes of red-belly and downy, but, judging from the labels and grouping in the collection of the Chicago Natural History Museum, these two species are sometimes placed in the same genus, Melanerpes. The major difference in foraging habits perhaps resides in the choice of live or dead branches, and the utilized areas of these two species are sometimes spatially segregated (see below).

The red-heads were by far the most numerous birds in the woods, and were decidedly aggressive, both among themselves and with other species (see also Orians and Willson 1964; Willson 1967). Of 87 interspecific aggressive encounters seen in winter, 35 were red-head vs. red-belly, 18 were red-head vs. downy, and 13 were red-head vs. Yellow-shafted Flicker (Colaptes auratus). In spring, 3 of 12 observed fights were red-head vs. red-belly, and 4 were red-head vs. flicker. The red-heads were generally active in initiating actual conflict, and usually dominated the other species, although sometimes red-bellies and flickers would hold their place by "passive" resistance.

With the possible exception of encounters between red-head and red-belly, interspecific conflict was seemingly unrelated to defense of territorial boundaries. Some of the red-belly winter areas were almost completely segregated from red-head territories, although red-bellies in other areas regularly intruded in red-head territories. Most of the conflicts occurred where the utilized areas of the two species overlapped. The range of movement of all other species involved in aggression overlapped completely with no sign of territorial segregation.

COMMENT

If male and female downies and red-bellies are treated as if the sexes were indistinguishable, and their foraging data (in per cent) lumped, usually the combined J' value is similar to that of one of the sexes (a difference of ≤ 0.50 was arbitrarily used as a criterion of "similar" since smaller differences seemed too small to be trusted and large ones, e.g., 1.0, gave much the same result) and greater than that of the other (8 of 10 comparisons, $0.10 > P > 0.05$, by χ^2). This is not what one would expect if the sexes subdivided each niche dimension of the species more or less equally. One might predict that each sex would be more specialized than the species as a whole, so that species J' values would exceed those of each sex. However, this is true only for downies in the spring, with respect to tree types and feeding sites. Instead, we find that one sex (either one) usually uses a given niche dimension broadly, while the other is specialized *within* the range of the other.

Remembering that this result is based on but two species, it is tempting to speculate that niche segregation of sexes is more likely to involve differences in degree of specialization to a similar range, while segregation of species may involve either differences in degree of specialization *or* actual subdivision of niche dimensions. As discussed in part by Selander (1966), this might, in fact, be predicted for several reasons: 1) the pressure of interspecific competition might often prevent any great divergence of the sexes; 2) the necessities of forming and maintaining a pair bond may bestow some selective advantage on similar feeding patterns; 3) the genetic and developmental background and selective pressures common to both sexes may often make divergence difficult. Schoener (1968), using different measures, has shown greater similarity between sexes than between species of lizards, even in the presence of several body-size categories within a species. In the present study, however, the amount of overlap between males and females of the two dimorphic species is not noticeably greater than between different species.

While all this is still very much in the realm of the arm-chairing addicts, it may provide another facet to the understanding of the evolution of sexual differences. Selander (1966) has nicely summarized the means available to a species of reducing intersexual competition. The present speculation suggests a refinement of the kind of divergence usually open to a species.

SUMMARY

A variety of significant differences in habitat utilization of coexisting species is presented. In both species in which sex is distinguishable in the field (Red-bellied and Downy Woodpeckers), foraging behavior of males and females is as distinct, within the limits of measurement, as that of other species. A speculation based on these data, however, suggests that the kinds of differences between the sexes of a species may often differ from those between species.

ACKNOWLEDGMENTS

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