LABORATORY STUDIES OF FORAGING IN FOUR BIRD SPECIES OF DECIDUOUS WOODLAND

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Abstract.—In an indoor aviary containing 60 American elm branches of 6 different diameters (0.5, 1.0, 2.5, 5.0 ,10.0, 20.0 cm), Carolina Chickadees, Tufted Titmice, male and female White-breasted Nuthatches, and male and female Downy Woodpeckers were allowed to forage singly under controlled circumstances. Each species had a particular and unique preference for branch size and branch surface. Variation occurred among the individuals of each species or sex, and differences between the sexes were found in branch sizes used by woodpeckers and branch surfaces selected by woodpeckers and nuthatches. Nuthatches alone seemed partially to select branch size by total available surface area; they also showed the greatest diversity in use of the three branch surfaces (top, sides, bottom). Differences among species in their use of different branch sizes and surfaces and in the extent to which their behavior changed with experience generally supported Morse's (1974) hypothesis that socially subordinate species are behaviorally more plastic in thier foraging and occupy a broader fundamental niche. *Received 29 February 1980, accepted 8 October 1980.*

Why do birds look for food the way they do? In studies of wild birds in nature, various workers have shown that foraging behavior can be controlled by variation in food distribution and abundance (e.g. Gibb 1954, Charnov et al. 1976), habitat type (Morse 1970), weather (Grubb 1975, 1977, 1979; Austin 1976), interspecific social environment (Morse 1974), season of the year (Travis 1977), and time of day (Rubenstein et al. 1977). How proximity of predators might influence avian foraging has not been studied systematically, but foraging activity in other taxa (e.g. crayfish, Stein and Magnuson 1976; fish, Milinski and Heller 1978) changes in the presence of predators. An important consideration is that each of these studies emphasizes only one or two of the many environmental factors that might be influencing foraging but does not control any of the others.

Concurrently, a large literature has accumulated concerning the ways by which avian communities partition resources (e.g. Willis 1966; Root 1967; Cody 1968, 1974; Willson 1970; Austin and Smith 1972; Alatalo and Alatalo 1979). The general thrust of these studies has been to explain such competition-reducing mechanisms among species as horizontal and vertical stratification of foraging sites, temporal differences in foraging activity, variation in foraging rates, and disparities in parts and sizes of vegetative substrates used. Such works about competition and realized niches (*sensu* Hutchinson 1957) have usually not considered the likelihood that factors other than the composition of their foraging guild could significantly control the food-seeking techniques of species.

Field observations of avian foraging behavior could be confounded by such un-controlled variables as sex, age, presence of conspecifics and competitor species, hunger state, food distribution and abundance, habitat type, weather, proximity of

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predators, time of day, and season of the year (Grubb 1979). Laboratory studies present the opportunity to control such variables, and the more elegant of these have offered birds different quality foods (Gass 1978) or food hidden in different places (Partridge 1976a, b).

The winter foraging behavior of four species resident in Ohio woodlands, the Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*P. bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), and Downy Woodpecker (*Picoides pubescens*), was studied in an indoor aviary in which all the above variables, except age and, in two species, sex, were known and controlled. Records were taken on branch sizes and branch surfaces (top, sides, bottom) selected by a bird searching for food.

The objectives of this study were to determine: (1) whether individuals within a species (chickadee and titmouse) or within a sex (nuthatch and woodpecker) differ in their foraging behavior; (2) whether sexes of a species differ in foraging; (3) whether species differ in their foraging behavior; (4) whether species select substrates on which to forage on a random basis or choose particular substrates; and (5) whether foraging changes with time in the absence of food reinforcement.

MATERIALS AND METHODS

Between 16 January and 1 March 1978, 10 Carolina Chickadees (CC) and 10 Tufted Titmice (TT) were captured in hardware-cloth treadle traps. Ten male and 10 female White-breasted Nuthatches (WBN) and 7 male and 7 female Downy Woodpeckers (DW) were captured between 3 January and 10 March 1979, using radio-controlled traps and Graves tree traps, respectively. Only 4 male and 4 female woodpeckers could be tested because of deaths during confinement (2 males) or refusal to forage in the aviary.

Chickadees and titmice cannot be sexed externally, and the birds in this study were not sacrificed or laparotomized, so for analysis the chickadees were considered one group, the titmice another, and the nuthatches and woodpeckers were divided into male and female groups. All birds tested were at least 6 months old and had had at least 8 weeks' experience foraging in deciduous woods during the no-leaf season.

Each bird was observed singly in an aviary constructed in a windowless cement-block building on The Ohio State University campus, Columbus, Ohio. Aluminum pipes formed the supports of the 3.1 × 4.3 × 2.8-m-high aviary, which was enclosed with polypropylene netting and lined with opaque black plastic. Two rows of three 40-W fluorescent lights provided illumination inside the aviary. At one end of the aviary was a 3.1 × 1.0 × 2.8-m-high annex, separated from the main aviary by netting only; its outside walls were also lined with plastic. A 5-cm × 3.1-m American elm (*Ulmus americana*) branch extended across the annex 1.5 m from the floor and could be seen but not reached by birds in the main chamber. The annex was empty throughout this study, but we anticipate using it in future studies when it will hold conspecifics, competitors, or predators.

The "habitat" inside the aviary consisted of 60 0.75-m-long American elm branches suspended on strings from the ceiling at 45° angles with their midpoints 0.9 m from the floor (Fig. 1). All branches were cut from live trees after leaf-fall in 1977. Six branch diameters were employed, measured midbranch: 0.5 cm (n = 15), 1.0 cm (n = 15), 2.5 cm (n = 9), 5.0 cm (n = 9), 10.0 cm (n = 6), and 20.0 cm (n = 6). Each branch was randomly assigned a position in a 5 × 12 matrix and a left or right 45° inclination. Further characteristics of the branches are shown in Table 1.

Inside the aviary, the "weather" conditions of temperature, light intensity, wind, and precipitation were held constant or within narrow ranges, and food, conspecifics, competitors, and predators were absent. Temperature in the aviary ranged from 23–28°C for the chickadees and titmice and from 19–23°C for the nuthatches and woodpeckers. To ensure that the aviary was devoid of prey items, we carefully examined each branch and removed from bark crevasses the insect adults, larvae, and eggs we found. Then we let pretest birds of each species search the branches for 2 h. No bird was seen to find any food during testing.

To standardize hunger, each bird was fasted for 1–2 h after capture, with water *ad libitum*, then introduced singly into the aviary between 0900 and 1200. The longer fasting times occurred when two birds were tested in one morning. As fasting intervals were similar for all species, the effect of food
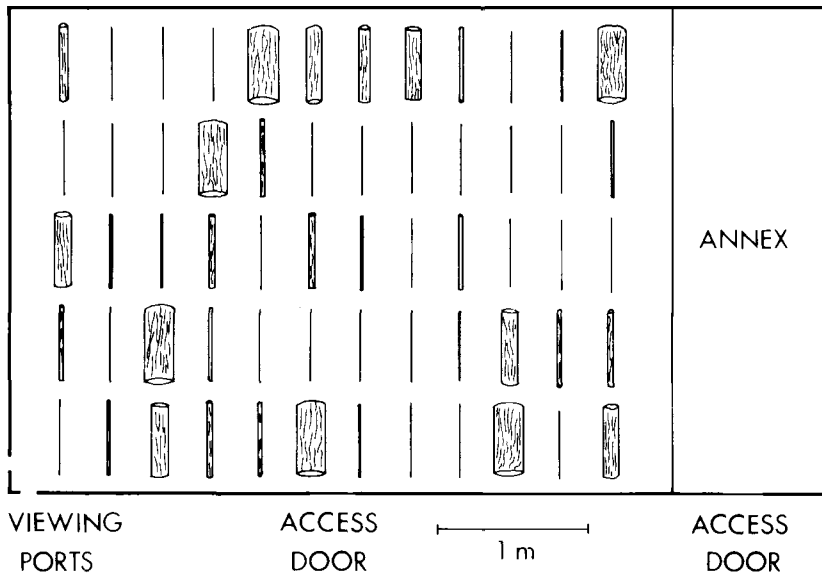
Fig. 1.   Overhead view of the aviary showing the 60 branches of six diameter classes. Ceiling lights and the strings supporting branches are not shown. Although the branches appear horizontal in the figure, they were hung at 45° angles (see text).

deprivation was probably more severe for chickadees, which weighed about 10 g, than for the nuthatch (about 21 g), titmouse (about 24 g), or woodpecker (about 25 g). The chickadees and titmice were tested on the day of their capture; nuthatches and woodpeckers were held overnight and tested the following morning.

Behavior in the aviary was observed through two 1 × 5-cm slits in the plastic lining, and observations were tape-recorded at a whisper. Birds appeared unaffected by our presence during their testing. After a bird had landed on the branches 200 times, or after 60 min, it was removed from the aviary, weighed, banded, and released at the site of its capture. Each individual was used only once. After each test, bark flakes dislodged from the branches by the foraging bird were removed by vacuuming the cement floor of the aviary.

For each branch on which a bird looked for food, records were taken on diameter class and branch surface (top, sides, or bottom). Branches were divided visually into top, side and bottom quadrants, where the top side faced the ceiling and the bottom side faced the floor. A bird was recorded as foraging in one of the quadrants when its head and feet were in that quadrant. The landing point on each branch was taken as the measure of a bird's preference for foraging site. When, periodically, a forager moved around a branch to search for prey in an additional quadrant, this behavior was not recorded. Thus, our records of branch surface selection are subject to some degree of error.

Analyses were accomplished using Chi-square tests (Runyon and Haber 1971), and we accepted significance at the 0.05 level.

TABLE 1.   Characteristics of the American elm branches in the aviary.

Diameter (cm)	Number	Total length (m)	Length ratio	Total surface area (m²)	Area ratio
0.5	15	11.25	2.5	0.18	1.0
1.0	15	11.25	2.5	0.35	1.9
2.5	9	6.75	1.5	0.53	2.9
5.0	9	6.75	1.5	1.06	6.0
10.0	6	4.50	1.0	1.41	8.3
20.0	6	4.50	1.0	2.83	17.8

RESULTS

Within 2 min of their introduction into the aviary, the nuthatches and wood-peckers commenced searching the branches for food. Chickadees and titmice delayed somewhat longer, but all began foraging within 15 min. Detailed descriptions of each bird's foraging behavior may be found in Pierce (1979).

Differences among individuals.—During the course of 200 landings, the 10 Car-olina Chickadees selected significantly different sets of branch sizes ($P < 0.01$). Members of this species also differed significantly in the proportions of landings on sides and bottoms of branches (the two branch-surface categories were lumped be-cause they were so seldom used) and on the tops ($P < 0.01$; Table 2).

Significant differences in branch size selection occurred among the 10 Tufted Titmice ($P < 0.01$). As all 10 titmice virtually ignored the sides and bottoms of the branches, there were no significant differences among individuals in surfaces scanned for food ($P > 0.30$; Table 2).

Viewed intrasexually, individual male White-breasted Nuthatches selected sig-nificantly different sets of branch sizes ($P < 0.01$), as did the females ($P < 0.01$). Because several nuthatches moved too rapidly for us to record their branch surface selections accurately, we have complete records for only seven males and eight females of this species. During 200 landings on branches, the seven male nuthatches showed no significant variation in selection of branch surfaces ($P > 0.30$). By con-trast, female nuthatches differed significantly in their choices of branch surfaces ($P < 0.01$; Table 2).

Individual male Downy Woodpeckers selected significantly different sets of branch sizes ($P < 0.01$), as did individual females ($P < 0.01$). Male ($P < 0.01$) and female ($P < 0.01$) woodpeckers also differed intrasexually in selection of branch surfaces (Table 2).

Differences between sexes.—There were no significant differences in branch size selection by male and female nuthatches ($P > 0.50$). The sexes varied significantly in their use of branch surfaces ($P < 0.01$), however, the males preferring the bottoms and the female preferring the sides (Fig. 2).

Male and female Downy Woodpeckers differed significantly in branch size selec-tion ($P < 0.01$). The cells for 5- and 20-cm branches in the Chi-square contingency table contributed 92% of the χ^2 value, indicating strong sexual variation in preference for these branch sizes. Females used the 5-cm branches and males the 20-cm branch-es much more than did the opposite sex. The sexes also differed in their use of branch surfaces ($P < 0.01$), with the males spending more effort on sides and bot-toms.

Differences among species.—Intraspecific variation notwithstanding, the four species selected branch sizes that differed significantly in the aggregate ($P < 0.01$). Examination of the values in the 4 (species) × 6 (branch sizes) contingency table showed that each species used one unique size markedly more than expected. These pairings, evident in Fig. 3, were Carolina Chickadee—1.0 cm, Tufted Titmouse—2.5 cm, Downy Woodpecker—5.0 cm, and White-breasted Nuthatch—20.0 cm.

There was considerable variation among the four species with respect to use of the three surfaces of the branches ($P < 0.01$; Fig. 2). Responses ranged from the nearly total dependence on branch tops by the titmouse to only about two-thirds of landings there in the nuthatch.

TABLE 2. Branch surfaces selected by each individual Carolina Chickadee, Tufted Titmouse, male and female White-breasted Nuthatch, and male and female Downy Woodpecker, shown as percentages of landings.

| Species	Branch surface	Individual										χ^2 (df)	P
		1	2	3	4	5	6	7	8	9	10		
CC	Top	85	87	93	92	93	90	87	99	92	98	45 (9)	<0.01
	Sides	12	8	6	7	6	7	11	1	7	2		
	Bottom	3	5	1	1	1	3	2	0	1	0		
TT	Top	100	99	100	100	100	99	100	100	99	98	10 (9)	>0.30
	Sides	0	1	0	0	0	1	0	0	0.5	2		
	Bottom	0	0	0	0	0	0	0	0	0.5	0		
♂ WBN	Top	61	69	70	69	65	65	66				5 (6)	>0.30
	Sides	24	25	26	24	26	23	25					
	Bottom	15	6	4	7	9	12	9					
♀ WBN	Top	62	77	69	74	71	39	54	48			109 (7)	<0.01
	Sides	29	20	25	20	24	38	32	41				
	Bottom	9	3	6	6	5	23	14	11				
♂ DW	Top	58	75	62	69							15 (3)	<0.01
	Sides	30	22	27	28								
	Bottom	12	3	11	3								
♀ DW	Top	96	87	72	74							35 (3)	<0.01
	Sides	4	12	25	21								
	Bottom	0	1	3	5								
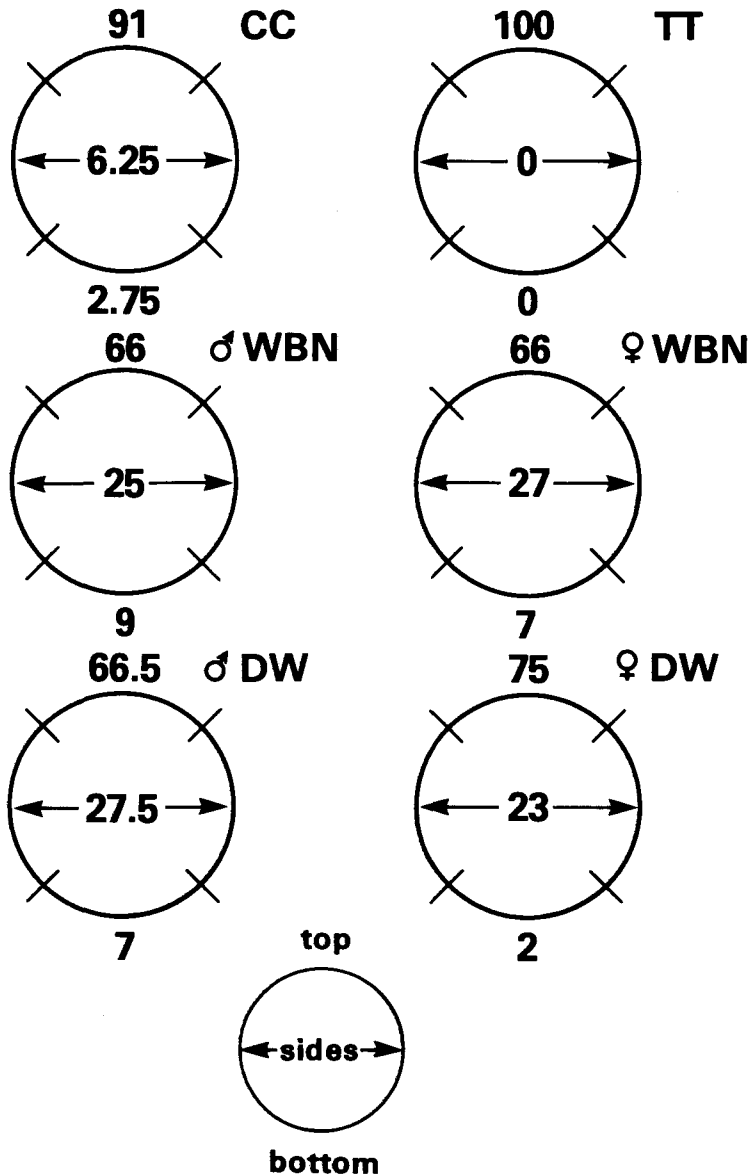
Fig. 2. Branch surfaces selected by Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.

Comparison with random selection.—If these four species normally forage without preference for particular branch sizes, branch-size selection in the aviary should have been proportional to the total lengths or total surface areas of the six branch sizes. Branch length and surface area ratios are given in Table 1. For each of the four species the distribution of landings differed significantly from that expected based on total lengths of the various branch sizes ($P < 0.01$; Fig. 4). Chi-square comparisons of landings expected from the ratio of branch surface areas with those
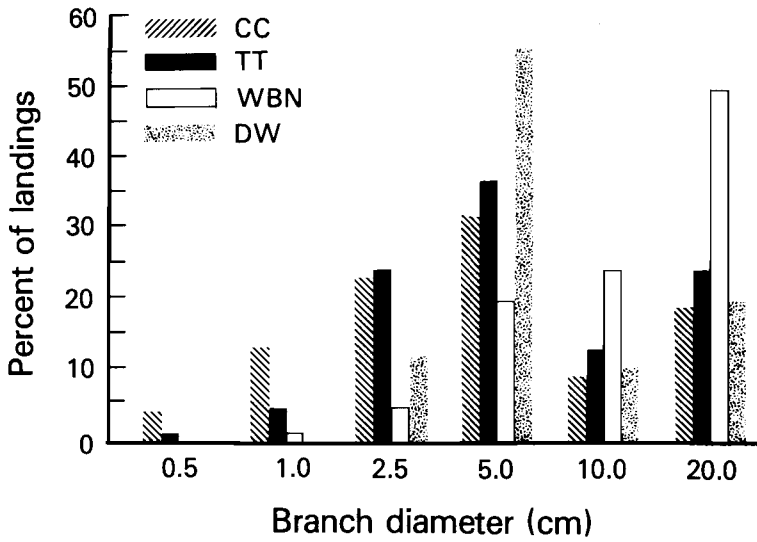
Fig. 3.   Branch sizes selected by Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers, shown as median percentages of the total landings.
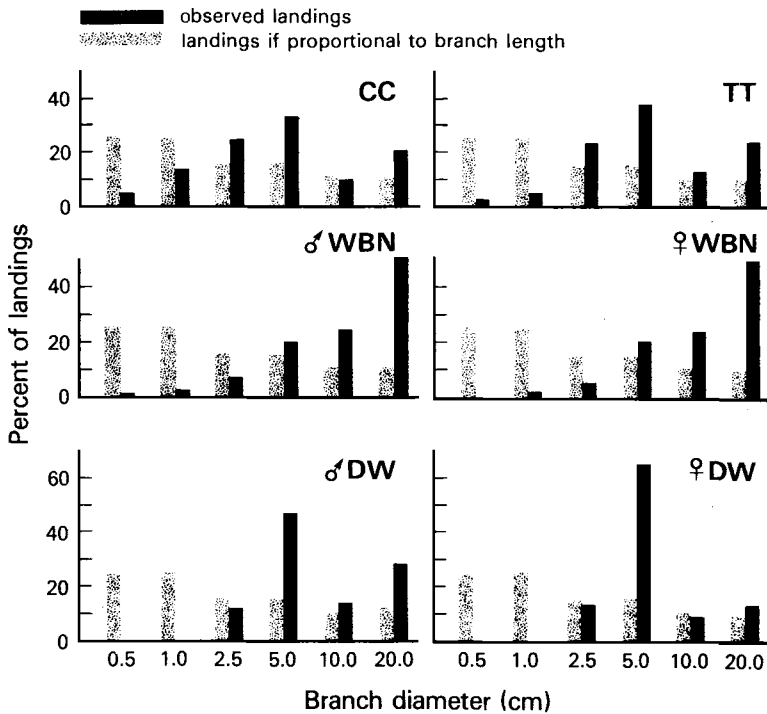

Fig. 4.   Comparison of observed selection of branch size, shown as percentages of all landings, with that expected if landings had been proportional to branch lengths.
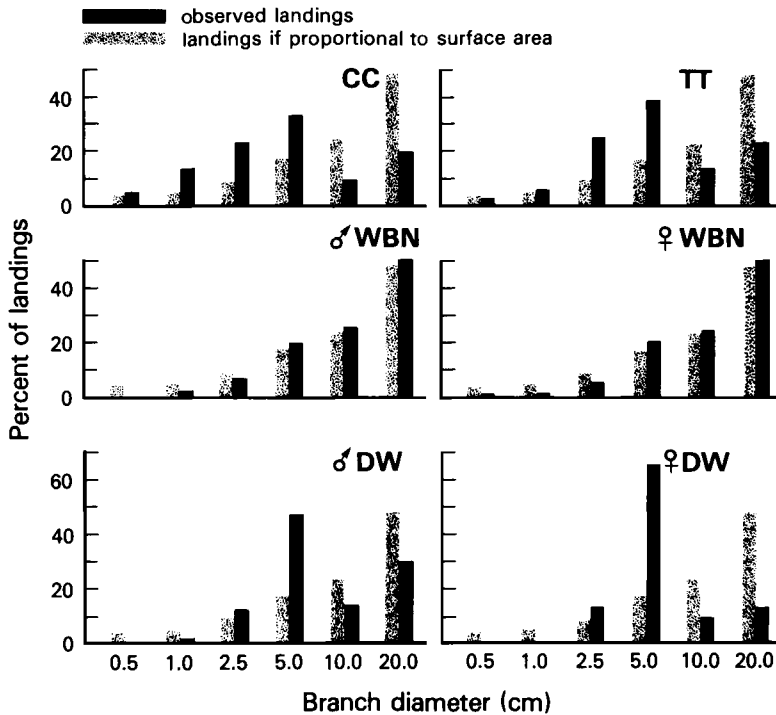
Fig. 5. Comparison of observed selection of branch size, shown as percentages of all landings, with that expected if landings had been proportional to branch-surface area.

observed also showed statistical significance for all species (P's $<$ 0.01). While it is clear from Fig. 5 that chickadee, titmouse, and woodpecker landings in no way resemble the proportions of surface areas, however, the nuthatch landings do. We found in the contingency table for this last species that 72% of the χ^2 value came from the cells for 0.5- and 1.0-cm branches. Figure 5 also suggests that, while they avoided these small branch sizes, the nuthatches used the four larger diameters proportional to their surface areas.

If the birds had no foraging preference for a particular branch surface, landings should have been proportional to the relative areas of tops (25%), sides (50%), and bottoms (25%). This was clearly not the case, as over the course of 200 landings all four species preferred to forage on the top surfaces (all P's $<$ 0.01; Fig. 6).

Variation with experience.—As the branches were devoid of prey, it was possible to determine, by comparing use of the six branch sizes during the first and last sets of 50 landings, whether birds responded to the lack of food reinforcement by changing their selection of branch sizes and surfaces. The chickadees, titmice, and nuthatches all significantly changed their branch-size preferences between landings 1–50 and 151–200 (P's $<$ 0.01). These species moved with experience toward the large diameters (Fig. 7). By contrast, branch-size selection in the Downy Woodpecker appeared unaffected by experience (P $>$ 0.50).

The χ^2 values obtained (df = 5) can be used to compare the magnitude of the
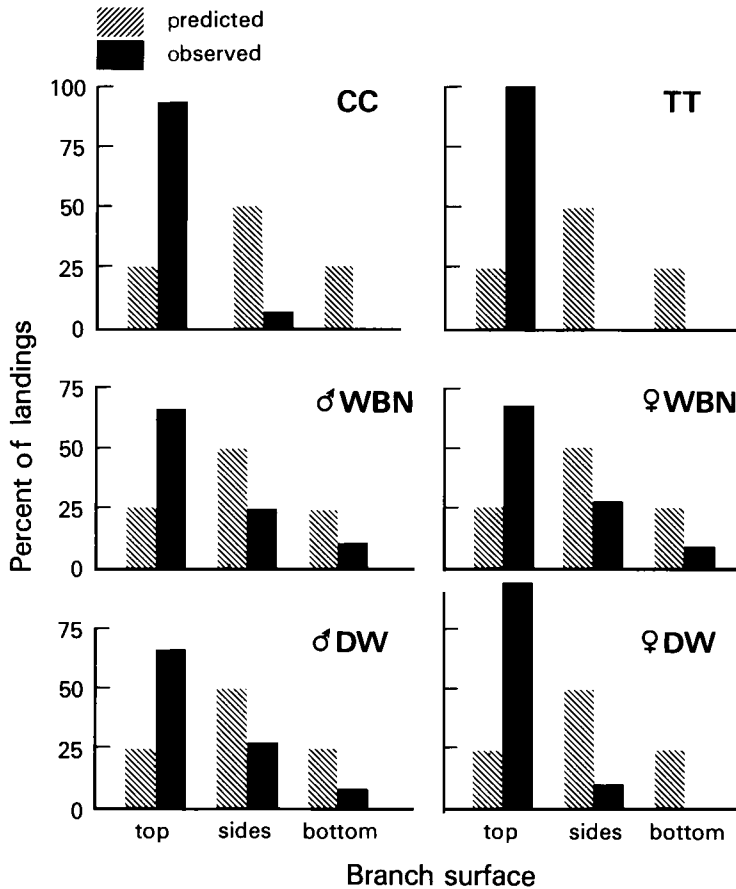
Fig. 6. Comparison of the observed percentages of landings on the three branch surfaces with percentages expected if birds had been responding proportional to available surface area.

shift with experience in the four species: these were 96, 49, 34, and 4, respectively, in the chickadee, nuthatch, titmouse, and woodpecker.

Changes in branch-surface preferences between landings 0–50 and 151–200 could be analyzed only for three species; titmice virtually ignored branch bottoms and sides (Fig. 3), so for this species the condition of the Chi-square procedure that all cells have expected values greater than or equal to 5 when df = 1 could not be met (Runyon and Haber 1971). Chickadees and woodpeckers shifted their preference for foraging surface significantly (P's < 0.01; Fig. 8), but the nuthatch did not (P > 0.50; Fig 8). Chi-square values of 15, 10, and 0.18 for the chickadee, woodpecker, and nuthatch, respectively, indicate the magnitude of the shift in branch-surface preference for each species.

DISCUSSION

Individual differences.—Except for branch-surface selection by titmice and male nuthatches, significant differences occurred among the birds of each sex and each species in use of branch sizes and surfaces. This result is of interest, because field
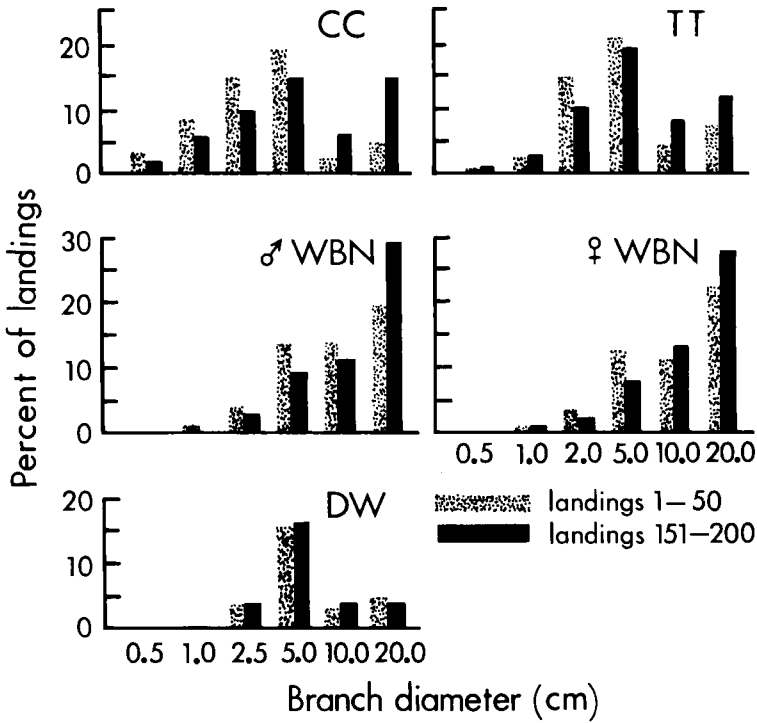
Fig. 7.   Comparison of branch sizes selected during the first 50 and last 50 landings of Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.
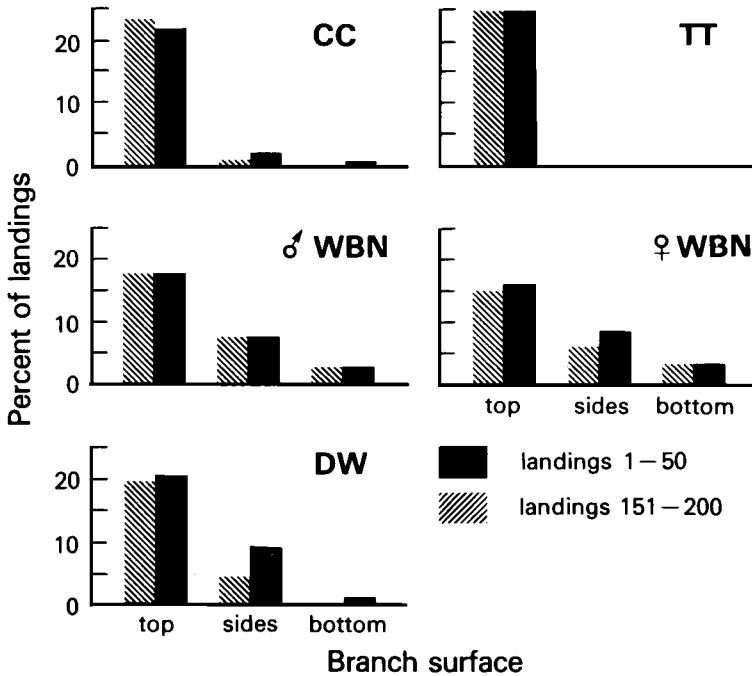

Fig. 8.   Comparison of foraging on the three branch surfaces in the first 50 and last 50 landings of Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.

studies of avian foraging routinely deal with individually unidentified birds and lump all sightings of a species for analysis (but see Holmes et al. 1978). Several factors may have contributed to these individual differences. Although an attempt was made to standardize hunger state, the amount of food chickadees and titmice had ingested before capture was unknown, and the length of the pretrial holding period varied from 1–2 h. There appears to be no evidence of how hunger state might influence foraging of free-ranging birds, but food deprivation does seem to affect the behavior of Pigeons (*Columbia livia*) and Chickens (*Gallus gallus*) (e.g. Levine 1974).

From field studies of readily sexed birds, we know that males and females can differ in such foraging techniques as branch-size selection (e.g. Downy Woodpeckers, Jackson 1970, Kilham 1970, Kisiel 1972, Williams 1975; and White-breasted Nuthatches, McEllin 1979). Carolina Chickadees and Tufted Titmice cannot be sexed externally, and, as the birds were not sacrificed or laparotomized, the question remains whether sex differences contributed to the observed variations among individuals in the two parids.

In some quite different birds, foraging techniques and success change with age (e.g. pelicans, Orians 1969; herons, Recher and Recher 1969). All the animals we tested were at least 6 months old and had had at least 8 weeks' experience foraging in deciduous woods during the no-leaf season. They could not be aged, however, and the possibility exists that birds of the year may have differed behaviorally from their elders.

Differences between sexes.—The nuthatch sexes selected the same proportions of branch sizes in our aviary, while McEllin's (1979) field results show males foraging on large diameter substrates and females on smaller branches. Because our birds foraged alone, while McEllin's did so in the company of the opposite sex, social dominance effects may account for the disparity.

In the aviary, the Downy Woodpecker sexes differed significantly in branch-size selection, with females using small (5 cm) and males the largest (20 cm) branches. Field studies (Jackson 1970, Kilham 1970, Kisiel 1972, Grubb 1975, Williams 1975) in other parts of North America have found sex-specific foraging in this species, but with males, not females, preferring smaller substrates. While our small sample size calls for caution in interpreting our laboratory results, we do note that also in the congenic Three-toed Woodpecker (*Picoides tridactylus,* Hogstad 1976) males use large substrates and females the smaller ones. We are currently examining the behavior of free-ranging Downy Woodpeckers here in Ohio (Peters and Grubb in prep.), with an eye to resolving this inconsistency between laboratory and field results.

Differences between species.—Partridge (1976b) watched isolated Blue Tits (*Parus caeruleus*) and Coal Tits (*P. ater*) search for food items contained in five types of artificial containers arranged on an indoor experimental tree made of dowels. The deciduous-dwelling Blue Tits and the conifer-dwelling Coal Tits have different foraging techniques in the field and maintained those differences in her laboratory study. Each species preferred to use the foraging technique that it employs in the field, and each was more efficient than the other at its preferred foraging technique.

The behavior of the four species we studied in controlled surroundings lends additional support to the model that avian species living together have different inherent preferences. Each species specialized more than expected on a different branch size, and the four used different proportions of branch sides and bottoms.

Morse (1974) hypothesized that interspecific social behavior is an important determinant of fundamental niche (*sensu* Hutchinson 1957) breadth. He proposed that social dominance among species frequently plays a major role in resource partitioning among mobile animals, that subordinates have considerably broader fundamental niches than their dominants, and that specialist dominants and high levels of niche overlap should result in guilds whose members show an inverse relationship between dominance rank and fundamental niche breadth.

The interspecific dominance hierarchy in this guild is Downy Woodpecker > White-breasted Nuthatch > Tufted Titmouse > Carolina Chickadee (Morse 1970). If we assume that a broad fundamental niche is indicated by a large number of preferred branch sizes and wide use of all branch surfaces, then this study supports Morse's hypothesis (Fig. 2). The parids displayed the most attributes of species with a broad fundamental niche and are subordinate to the nuthatches and woodpeckers. The blurring of distinctions with regard to niche size between the two parids and between the nuthatches and woodpeckers may have resulted from the absence of social influence while the tests were conducted.

Differences from random foraging.—Our statistical procedure indicated that all four species actively selected certain branch sizes and surfaces on which to forage. Results for the White-breasted Nuthatch (Fig. 5), however, lead us to an alternative premise, that, while this species avoids branch sizes $\leqq$ 1 cm in diameter, it uses all larger substrates in proportion to the abundance of their surface areas in the habitat.

In a temperate deciduous woodland, large diameter tree trunks and branches may comprise the greatest proportion of available surface area for foraging. For species such as American elm, tulip (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and box elder (*Acer negundo*) bark furrowedness may be an important cue to the foraging insectivorous bird (Travis 1977). The rough-barked surfaces of trees are important places for insect larvae to overwinter (MacLellan 1959), and the significance of bark crevices as food sources for the Downy Woodpecker has been discussed by Jackson (1970) and Travis (1977). Nuthatches cache food in bark crevices (Bent 1948); perhaps bark furrowedness, as well as surface area, would be selected by nuthatches. Although no precise measurements were made of bark furrowedness, the relative abundance and depth of crevices seemed to increase with increasing branch diameter.

In nature it is not possible to ascertain whether use of a particular branch size differs from random or whether branch size selection is affected by social pressure from more dominant species in a foraging guild. Thus, comparison of the branch-size preferences demonstrated in this study with those reported from field observations may be informative.

The chickadees' avoidance of 0.5-cm branches was unexpected, because during the winter in Ohio woodlots this species uses substrates less than 1 cm almost exclusively (Grubb unpubl.). Extensive use of twigs by chickadees in nature may occur only because twigs are so abundant relative to larger diameter branches. Also, in nature, chickadees may be forced from preferred 1.0- and 2.5-cm branches by social pressure from the larger, dominant Tufted Titmouse (Morse 1970).

Willson (1970) reported greater use of small branches (<7.5 cm) by free-ranging White-breasted Nuthatches than occurred in our study, although in both cases large (>7.5 cm) branches were preferred. We do not know the relative abundances of various branch sizes in Willson's study area, however.

Differences with experience.—With lack of food reinforcement from the branches, all four species changed foraging preferences for the various branch sizes or surfaces. That subordinates should show more plasticity of behavior was among Morse's (1974) predictions of the effect of social dominance on foraging. If shifts in substrate preferences shown by the birds in this study are appropriate measures of behavioral plasticity, Morse's prediction is partially upheld. The magnitudes of the χ^2 values generated from comparison of branch-size selection between landings 0–50 and 151–200 show that, as predicted, the subordinate chickadee's searching behavior was most responsive to experience, the dominant woodpecker's foraging was least labile, and the nuthatch and titmouse were intermediate. The subordinate chickadee also changed branch-surface selection most with experience. While the reversal in plasticity of surface selection between the nuthatch and woodpecker was counter to prediction, the small number of woodpeckers tested could have been responsible.

The degree of correspondence between behavior in the artificial environment of our aviary and that of free-ranging birds is open to question. It is clear that additional field study checking the validity of these laboratory findings will be necessary.

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