SEXUAL AND SEASONAL DIFFERENCES IN FORAGING OF LADDER-BACKED WOODPECKERS

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Differential foraging behavior by the sexes has been noted in several woodpeckers of the genus *Dendrocopos* (Kilham 1965, 1970, Ligon 1968a, 1968b, Jackson 1970, Short 1971, Willson 1970, Koch et al. 1970, Kisiel 1972). One species, the Ladder-backed Woodpecker $(D. \ scalaris)$ has received little attention although there is a suggestion that the sexes forage in different ways (Short 1971). In this paper, I present data on the foraging of this species gathered from April 1970 through September 1971 on the Santa Rita Experimental Range, Pima Co., Arizona. In addition, comparisons are made with other species of the genus.

STUDY AREA AND METHODS

Birds were studied in disturbed desert grassland on the northwest slope of the Santa Rita Mountains southeast of Sahuarita. The vegetation was dominated by mesquite (*Prosopis juliflora*), palo verde (*Cercidium microphyllum*), catclaw (*Acacia greggii*), hackberry (*Celtis pallida*), and cholla cacti (*Opuntia fulgida* and *O. spinosior*).

When a foraging woodpecker was encountered, I recorded the following data: plant species, height of plant, horizontal and vertical position of the bird within the plant, perch size, and method of foraging. The latter was categorized as probe (foraging within crevices in bark, or among the bases of leaves or spines), peck (subsurface foraging using forceful blows of the bill), or gleaning (foraging from the surface of bark or leaves). Horizontal and vertical



FIGURE 1. Plant species used for foraging by Ladder-backed Woodpeckers (sexes differ significantly in breeding and winter seasons).



FIGURE 2. Height of vegetation foraged in (sexes differ significantly except in post-breeding season) and foraging height (sexes differ significantly throughout) of Ladder-backed Woodpeckers (sample sizes as in fig. 1).

positions were recorded as percent of the distance from the trunk (axis) to branch tip and from the top of the tree to the ground, respectively. These data were recorded only on the initial sighting of the bird and only if I had not disturbed the bird. A total of 210 observations were made (102 for male, 108 for female) on about 6 pairs of birds.

I divided the year into three periods for comparisons: April-June, the breeding season; July-September, the post-breeding season (also the rainy season with a great increase in insect populations); and October-March, the winter season. Data were treated statistically using chi-square tests (P < 0.05) on the original numerical data using only pairs of cells with non-zero entries.

RESULTS AND DISCUSSION

The sexes were effectively separated in their foraging through most of the year by using significantly different substrates. In all but the post-breeding season, males foraged principally in chollas and females in mesquite (fig. 1). During the post-breeding season both sexes foraged predominantly in mesquite. Females tended to forage in significantly larger plants (except post-breeding) and at a significantly greater height than males (fig. 2).

Males foraged mainly by probing into crev-

ices and among cholla spines except from July to September (the post-breeding period) when there is considerable pecking. Females differed in that they foraged both by pecking and gleaning (fig. 3). The method of foraging was significantly different between sexes except during winter.

The sexes also differed significantly in the region of the tree or shrub and the size of the foraging perch used (figs. 4 and 5); males used larger, more central trunks and branches, whereas females more often foraged on smaller peripheral branches and twigs of mesquites. Foraging data presented here further demonstrate the complexity of the foraging niche of Ladder-backed Woodpeckers woodpeckers. not only differed in foraging mode and site (as do several other woodpecker species), but also varied seasonally as did Downy Woodpeckers (D. pubescens) studied by Jackson (1970) and White-headed Woodpeckers (D. albolarvatus) investigated by Ligon (1973).

Primary niche segregation was through the use of different plant species. Females foraged nearly exclusively in mesquites throughout the

		$\begin{array}{r} \text{Males} \\ \text{in chollas} \\ (N = 57) \end{array}$		$\begin{array}{rl} Males\\ \text{in mesquite}\\ (N = 40) \end{array}$		Females in mesquite (N = 98)
Method	probe peck glean	$61.4 \\ 28.1 \\ 10.5$	*	20.0 47.5 32.5	n.s.	13.3 38.8 48.0
Perch size	trunk branch twig	57.9 35.1 7.0	*	$15.0 \\ 80.0 \\ 5.0$	n.s.	$1.0 \\ 74.5 \\ 24.5$
Perch size (mm)	$\begin{array}{c} 2.5 - 12.5 \\ 12.5 - 25 \\ 25 - 50 \\ 50 - 75 \\ > 75 \end{array}$	3.529.838.626.31.8	*	$25.0 \\ 12.5 \\ 40.0 \\ 5.0 \\ 17.5$	*	$61.2 \\ 15.3 \\ 19.4 \\ 4.1 \\$
Percent from top	0-10 20-30 40-50 60-70 80-100	8.8 15.8 26.3 36.8 12.3	n.s.	10.0 15.0 35.0 25.0 15.0	*	$9.2 \\ 58.2 \\ 14.3 \\ 16.3 \\ 2.0$
Percent from axis	0-10 20-30 40-50 60-70 80-100	57.9 3.5 3.5 8.8 26.3	*	7.5 12.5 15.0 50.0 15.0	*	$6.1 \\ 7.1 \\ 7.1 \\ 26.5 \\ 53.1$
Foraging height (m)	$\begin{array}{c} 0-1.0\\ 1.1-2.0\\ 2.1-3.0\\ 3.1-4.0\\ 4.1-5.0\end{array}$	87.7 12.3 —	*	$15.0 \\ 25.0 \\ 40.0 \\ 12.5 \\ 7.5$	*	$3.1 \\19.4 \\23.5 \\46.9 \\7.1$

TABLE 1. Comparison (percent) of male and female Ladder-backed Woodpecker foraging.*

^a Statistical comparisons were made between males foraging in chollas and males foraging in mesquite, as well as between the latter and females foraging in mesquite. An asterisk indicates a significant difference (P < 0.05); n.s. indicates no significant difference.

Species of Dendrocopos	Plant species ^a	Modea	Site ^a	Season	Location	Source
villosus	X	X		winter	New Hampshire	Kilham 1965
• • • • • • • • • • • • • • • • • • • •	õ	ō	Х	winter	California	Short 1971
	Х	0	Х	winter	New York	Kisiel 1972
pubescens		_	Х	winter	New Jersey	Grubb 1975
	0		Х	winter	New Hampshire	Kilham 1970
	х	0	Х	entire yr.	Kansas	Jackson 1970
	х	0	Х	winter	Illinois	Willson 1970
	Х	Х	Х	spring	Illinois	Willson 1970
	х	Х	X	spring	Illinois	Williams 1975
	Х	Х	X	winter	New York	Kisiel 1972
borealis	0	х	Х	entire yr.	Florida	Ligon 1968a
	0		0	winter	Louisiana	Morse 1972
albolarvatus	0	—	Х	spring	California	Koch et al. 1970
	0	0	0	spring	Idaho	Ligon 1973
	0	0	0	summer	Idaho	Ligon 1973
stricklandi	0	0	Х	winter	Mexico	Ligon 1968b
arizonae	0	Х	Х	summer	Arizona	Ligon 1968a
nuttallii	0	0	Х	spring	California	Short 1971
scalaris	Х		Х	spring	California	Short 1971
	0	—	Х	winter	California	Short 1971
	Х	Х	Х	spring	Arizona	This study
	0	Х	Х	summer	Arizona	This study
	Х	0	Х	winter	Arizona	This study

TABLE 2. Extent of sexual differences in foraging of Dendrocopos woodpeckers.

^a An "X" indicates that the sexes differ, an "O" that there are no sexual differences, and a "-" that data are lacking or insufficient.



FIGURE 3. Method of foraging by Ladder-backed Woodpeckers (sexes differ significantly except in winter; sample sizes as in fig. 1).

year, while males foraged in chollas more than 75% of the time during the winter and breeding seasons. Over 60% of the foraging by males was in mesquites in the post-breeding season. There was also a shift in foraging by males during the post-breeding season to methods and sites resembling those of the female. Foraging patterns for females remained relatively constant throughout the year.

Because of differences in foraging substrate, other differences in foraging behavior were secondary and relatively unimportant in maintaining foraging niche segregation by the sexes. I can offer two possibilities, however, to explain these secondary differences: (1) these were imposed by the characteristics of and the prey available on the vegetation foraged in; or (2) these were the original means of sexual foraging segregation. The data suggest that a combination of both are responsible.

When foraging in mesquites, the sexes of Ladder-backed Woodpeckers differed in the site used although the method of foraging was similar (table 1). Males foraged lower and more towards the center on larger branches than females. When foraging in mesquites, males differed in nearly all criteria from when they foraged in chollas (table 1). Thus, although foraging patterns were modified by substrate (i.e., differences between males foraging in mesquites and males foraging in chollas), males foraged in different locations than females while foraging in mesquites.

The sexes of all species of *Dendrocopos* for which there are data (except for *D. albolarvatus* in Idaho and *D. borealis* in Louisiana during winter) differ in their site of foraging, whether or not they differ in species of tree



FIGURE 4. Relative position in vegetation of foraging by Ladder-backed Woodpeckers (sexes differ significantly except percent from top in breeding season and percent from axis in post-breeding season; sample sizes as in fig. 1).

foraged in or mode of foraging (table 2). Differences in site involve males foraging primarily on the trunk or larger branches and females more peripherally on smaller branches and twigs in *D. arizonae*, *D. stricklandi*, *D. nuttallii*, *D. villosus* and *D. scalaris* (Ligon 1968a, 1968b, Short 1971, this study) or males foraging more peripherally and females on larger perches in *D. borealis*, *D. pubescens* and *D. albolarvatus* (Ligon 1968a, Jackson 1970, Koch et al. 1970, Kilham 1970, Willson 1970, Kisiel 1972).

Sexual differences in plant usage depend on the availability of suitable plants on which to forage. Certain species (D. borealis, D. albolarvatus, D. stricklandi) which do not differ in this respect (table 2) were studied in communities with only one dominant tree species. In New Hampshire, both sexes of D. pubescens concentrated their foraging in one tree species having an abundant food supply (Kilham 1970). In more diverse plant communities, segregation is possible due to a greater diversity of available foraging sites, a lack of competition from other species of woodpeckers, or a wide variety of resources

		Season			
Variable	Sex	Breed- ing	Post- breeding	Winter	
Vegetation	\$.653	.667	.349	
	Ŷ	.081	.361	.160	
Height of plant	8	.649	.823	.524	
	ę	.475	.659	.424	
Foraging height	8	.525	.819	.498	
	ę	.827	.871	.632	
Percent from top	ð	.973	.886	.893	
	ę	.808	.869	.347	
Percent from axis	3	.554	.970	.910	
	ę	.897	.866	.501	
Perch size	ð	.819	.499	.779	
(qualitative)	Ŷ	.545	.606	.810	
Perch size	ð	.892	.970	.722	
(quantitative)	ę	.674	.722	.711	
Method	8	.819	.870	.978	
	ę	.870	.877	.978	

TABLE 3. Indices of foraging diversity (1') of

Ladder-backed Woodpeckers.*

^a Sample sizes as given in figure 1.



FIGURE 5. Perch size used by foraging Ladder-backed Woodpeckers (sexes differ significantly except qualitative perch size in post-breeding season; sample sizes as in fig. 1).

on several species of plants. In desert grassland there are few species of suitable plants on which to forage. Here, during the postbreeding rainy season, both sexes of *D. scalaris* foraged primarily in mesquite. In winter, when prey appeared to be less abundant and in the breeding season when there is a greater demand on the food supply to feed dependent young, the sexes foraged predominantly on different plant species.

Males appeared opportunistic, apparently using the most productive substrates, depending on time of year, and generally utilized more diverse foraging sites than females. To test this hypothesis, I calculated an index of diversity (J', see Pielou 1966 for discussion) for the eight sets of data for the three seasons (table 3). A small value of J' indicates a tendency towards specialization whereas a larger value indicates generalization. Values for males exceeded those for females in 15 of 24 comparisons. Males tended to be generalists in vegetation selection, height of vegetation used, perch size and position in the vegetation. Females were generalists only in foraging height. Mode of foraging of the two sexes showed similar generalizations. Generalization of foraging patterns by both sexes averaged greater during the post-breeding season especially among vegetation characteristics and position in the vegetation.

In the Downy and Red-bellied (*Centurus carolinus*) woodpeckers, Willson (1970) found that one sex used a particular niche dimension broadly (similar to the two sexes combined) while the other was more specialized within the range of the species. This also occurred in Ladder-backed Woodpeckers (16 of 24 comparisons, males using niche dimension broadly in 12 cases). The sexes did not divide the species' foraging niche equally, but inter-

sexual competition was reduced by the males using a wide range of sites and the females being more specialized. Some of the generalization of males undoubtedly was due to their use of a wider variety of plants than females. Hence, males must adopt different strategies imposed by the nature of foraging substrate (i.e., table 1) and/or prey. Thus, males are specialized as generalists. Their longer bill (exceeding that of females by 15%; Short 1968) may allow a greater range of food types. Since Ladder-backed Woodpeckers nearly always forage alone, it is unlikely that dominance of males affects foraging patterns as suggested for other *Dendrocopos* (Ligon 1968a, 1973, Kilham 1970).

SUMMARY

The sexes of Ladder-backed Woodpeckers differ in their foraging behavior in southern Arizona. Additionally, there are seasonal differences in foraging, especially by the males. Males tend to be generalists while females tend to specialize. Seasonal variation in foraging appears to depend on food availability and demand.

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