INTERSEASONAL AND INTERSEXUAL RESOURCE PARTITIONING IN HAIRY AND WHITE-HEADED WOODPECKERS

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ABSTRACT.—Foraging behavior in the closely related Hairy (*Picoides villosus*) and White-headed (*P. albolarvatus*) woodpeckers was examined in an area of sympatry to evaluate interseasonal and intersexual resource use. Similar foraging heights were observed for each species-sex sample during summer, but significant differences were evident during winter. Male and female White-heads maintained similar relative foraging heights between seasons, whereas male and female Hairies foraged relatively higher during winter. Use of tree species differed significantly for each class between seasons, except for male Hairies. Differences in foraging substrates and tree health also were noted interseasonally. All foraged at similar times of day during summer, but negative relationships occurred between times of foraging during winter; foraging times were significantly different between male Hairies and White-heads.

A general trend toward decreased overlap in foraging behaviors during winter was a reflection of concentration of foraging activities on live incense cedar (*Calocedrus decurrens*), especially by female White-heads. This change apparently was due to the presence of an abundant and accessible prey (incense cedar scale, *Xylococculus macrocarpae*) on cedar. Behavioral shifts in foraging activities may be related to the differential ability to extract prey as a function of bill morphology; such an idea can be extended to intersexual as well as interseasonal considerations. Thus, segregation of foraging activities in these two woodpecker species may be attributed to morphological differences and habitat complexity rather than to competitive interactions dictated by resource limititions. *Received 16 May 1986, accepted 13 October 1986.*

THE utilization and partitioning of resources by closely related, sympatric species of birds has attracted much study (e.g. see reviews by Schoener 1974, Eckhardt 1979, Rotenberry 1985). As a group, co-occurring species of woodpeckers (family Picidae) have received frequent attention (e.g. Kisiel 1972; Williams 1975; Conner 1980, 1981), possibly owing to the ease of observation and the occurrence of sexual dimorphism. Thus, woodpeckers make good subjects for evaluation of resource partitioning on both interspecific and intersexual levels (e.g. Kilham 1965, Ligon 1968, Austin 1976, Jenkins 1979, Williams 1980, Peters and Grubb 1983).

During preliminary studies of bird communities in the western Sierra Nevada, California, we noted the co-occurrence of two *Picoides* species in a mixed-conifer forest: the Hairy (*P. villosus*) and White-headed (*P. albolarvatus*) woodpeckers (Morrison et al. 1985, 1986). Sympatric species of woodpeckers differ greatly in size and in foraging habits (Short 1971). The two species considered here were described by Short (1971) as "ecologically separate" when sympatric, with *albolarvatus* occuring in "pine" and *villosus* in "other coniferous forest and mixed woods." We evaluated modes of resource partitioning by these two similar-size (by body mass; Dunning 1984) and closely related (Short 1971, 1982) species in an area typified by a ubiquitous mixture of five coniferous and one deciduous tree species. These data were analyzed on an intersexual and interseasonal basis to determine if methods of resource use and the magnitude of resource partitioning varied by sex, season, or both.

STUDY AREA AND METHODS

The study area was the Blodgett Forest Research Station (administered by the Department of Forestry and Resource Management, University of California, Berkeley), El Dorado Co., California. This 1,200-ha forest is located in the mixed-conifer zone (see Grif-

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fin and Critchfield 1972) at about 1,350 m elevation in the west-central Sierra Nevada. The forest is predominated by incense cedar (*Calocedrus decurrens*; 25% of total basal area, unpubl. data), white fir (*Abies concolor*; 21%), ponderosa pine (*Pinus ponderosa*; 19%), Douglas fir (*Pseudotsuga menziesii*; 15%), sugar pine (*P. lambertiana*; 10%), and California black oak (*Quercus kelloggii*; 8%). The forest has been divided into 5-40-ha compartments managed under various silvicultural systems. The forest is now mostly mature (>70 yr old) conifer.

During summer (early May to late July) 1983 and 1984, 24 compartments totaling about 420 ha were selected for study. During summer 1985 we selected 9 compartments, 7 of which differed from those used during 1983-1984; the 1985 study area totaled about 210 ha. Because access to much of the forest was limited during winter, a subset of 4 large compartments used during summer totaling about 100 ha was selected for study during winter (early November to mid-March) 1982-1983 and 1983-1984. Summer and winter sites were of similar age and tree-species composition.

The abundance of Hairy and White-headed woodpeckers is similar during winter (0.19 and 0.17 birds/count, respectively) and summer (0.13 and 0.08 birds/count, respectively) (Morrison et al. 1986). Other woodpecker species that occurred at Blodgett were Northern Flickers (*Colaptes auratus*), Red-breasted Sapsuckers (*Sphyrapicus ruber*), and Downy (*P. pubescens*) and Pileated (*Dryocopus pileatus*) woodpeckers (Morrison et al. 1986). Adequate data were not available, however, to analyze these species interseasonally or intersexually.

About 1,250 person-hours during summer and 700 person-hours during winter were spent observing foraging behavior. An observer walked systematically through a compartment recording data on birds as encountered; 10 different observers spent varying amounts of time recording data during the study. We divided our activities so that roughly equal time was spent in each compartment during each season. Data on only one individual of a species were recorded at a particular place and time regardless of the number of birds present. Data on only one or two species were recorded when observing flocking birds to minimize the potential problem of correlated activities of co-occurring individuals.

Except for winter 1982-1983, foraging activities were recorded for a minimum of 10 s to a maximum of about 30 s. For each individual we recorded date, time of day, species, sex, species of plant, foraging substrate (e.g. limb, trunk), time spent on each substrate, perch height, plant height, and type of foraging motion (e.g. glean, peck). This same information was recorded during winter 1982-1983, but observations were made on an individual every 30 s to a maximum of about 5 min (i.e. sequential observations). We modified our methods because analysis of sequential observations has certain statistical problems. Results of both techniques are comparable, however, given adequate sample sizes; our data exceeded this requirement (Morrison 1984). The presence of observers likely affected foraging activities. Because the initial sighting of a bird probably was biased toward conspicuous individuals, using only the first observation of an individual would not solve the problem associated with observer effects on foraging activities. We assumed that these problems influenced the data in a similar manner for all species and sexes. Because of problems concerning independence of data recorded sequentially, we were especially careful when interpreting results at P near 0.05.

We calculated resource overlap,

$$C_{xy} = 1 - \frac{1}{2}\left(\sum_{i=1}^{r} |p_{xi} - p_{yi}|\right),$$

where p_{xi} and p_{yi} are the proportional use of the ith resource state by the xth and yth species. C ranges from 0 (total dissimilarity) to 1 (total similarity) (Colwell and Futuyma 1971). A two-dimensional measure was calculated from a foraging tree-foraging substrate matrix. Calculating multidimensional resource overlap in this manner is preferable to using additive or multiplicative values (Alatalo 1982). We did not calculate three-dimensional matrices because cellular values would become too small for calculation of meaningful results (Alatalo 1982). These indices present simple summaries of data, but do not indicate statistical significance (although they may be biologically important). Therefore, we compared (for independence) the distribution of certain foraging activities for the various resource states between species and sexes using a Chi-square analysis (Fisher's exact test was used for small samples; see Norusis 1983). Further, through computer simulations, Ricklefs and Lau (1980) found that a difference of 0.1-0.2 was required to reject the null hypothesis that two overlap indices were drawn from the same sampling distribution. Therefore, we adopted the general rule that two indices must differ by at least 0.2 to merit discussion.

Resource partitioning may occur if species forage at different times (Schoener 1974). For this study we used a simple index of foraging time: assuming observers encountered birds at random, we calculated species- and sex-specific times of activity by determining the frequency at which birds were observed in 1-h periods. We then used Spearman's rank correlation (r_s) to determine if times of foraging activities were similar. Observers systematically surveyed birds throughout the day, which reduced potential biases in foraging activity times.

The external morphology of Hairy and White-

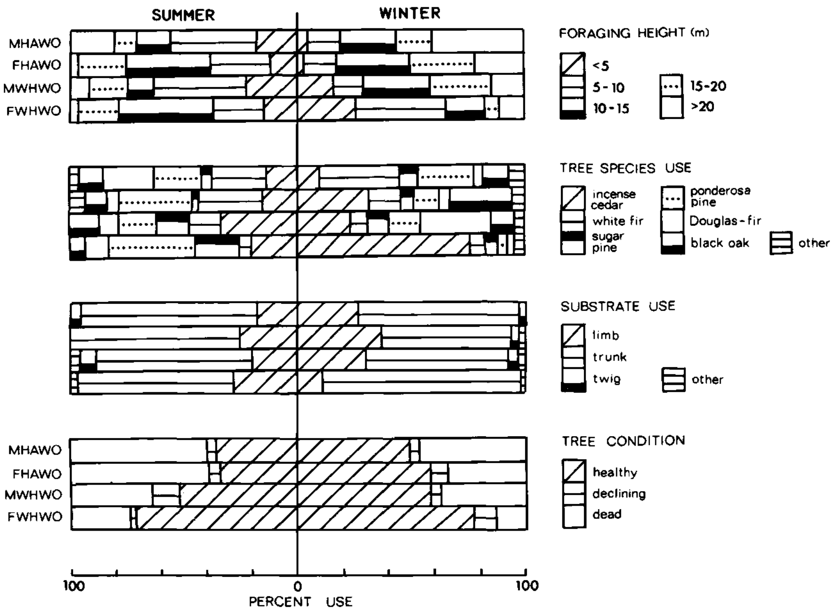

Fig. 1. Use of foraging heights, tree species, foraging substrates, and tree condition for male (M) and female (F) Hairy (HAWO) and White-headed (WHWO) woodpeckers during summer and winter at Blodgett Forest, California.

headed woodpeckers varies both interspecifically and intersexually (Grinnell 1902, Ridgway 1914, Ligon 1973, Dunning 1984). We supplemented these data by measuring the length of the exposed culmen of 10 individuals for each sex of the two woodpeckers using museum specimens from within the range of the subspecies occurring at Blodgett (A.O.U. 1957).

Analyses were conducted using SPSS× (SPSS 1983), except for the Chi-square tests, which were executed on the Number Cruncher Statistical System version 4.2 (J. L. Hintze 1985, Kaysville, Utah).

RESULTS

Foraging height.—The distributions of foraging activities by height categories (Fig. 1) were significantly (χ^2 test, $P < 0.01$) different between seasons for all but female Hairies ($P > 0.05$). Male White-heads had a more even distribution of foraging heights during winter relative to summer, when activities were concentrated between 5 and 10 m (Fig. 1). Males of both species exhibited high overlap (>0.7) during winter and summer (Table 1). Females of the two species showed a decreased overlap (>0.3 change) during winter, possibly because of differential concentration of activities, with Hairies occurring primarily (60%) at greater heights (>10 m) than White-heads (Fig. 1).

Mean foraging heights were similar for all samples during summer, but significant differences were evident during winter, when male Hairies foraged higher and female White-heads lower than was evident at other seasons (Table 2). Except for female White-heads, all others increased significantly their absolute foraging height during winter. A trend toward increased absolute height of the foraging tree also was observed during winter, except for female White-heads, which used significantly shorter trees during winter. The relative positions (foraging height/tree height ratio) of male and female White-heads were identical between seasons, however. In contrast, male and female Hairies foraged relatively higher in trees during winter (Table 2). Although all except female Hairies used smaller (diameter at breast height) trees during winter, only female White-heads showed a significant change. Because we report data for all tree species combined, no consistent relationship between the height and dbh of foraging trees can or should be taken from Table 2.

Tree-species use.—Male Hairies showed a similar use of tree species during summer (except for sugar pine, which was relatively low in all species-sex samples; Fig. 1). The other samples

TABLE 1. Foraging resource overlap for male and female Hairy and White-headed woodpeckers. Sample sizes are given in the Appendix.

		Comparison					
Resource	Season[a]	Male Hairy, female Hairy	Male Hairy, male White-head	Male Hairy, female White-head	Female Hairy, male White-head	Female Hairy, female White-head	Male White-head, female White-head
Foraging height	S	0.65	0.87	0.63	0.69	0.88	0.67
	W	0.78	0.73	0.56	0.85	0.55	0.66
Tree species use	S	0.74	0.70	0.59	0.66	0.64	0.70
	W	0.61	0.56	0.34	0.65	0.55	0.44
Substrate use	S	0.93	0.89	0.88	0.89	0.95	0.91
	W	0.87	0.93	0.82	0.93	0.71	0.75
Substrate condition	S	0.98	0.76	0.65	0.75	0.63	0.80
	W	0.87	0.91	0.66	0.97	0.79	0.76
Tree species by substrate	S	0.68	0.55	0.56	0.50	0.63	0.61
	W	0.61	0.50	0.35	0.60	0.53	0.41

[a] S = summer, W = winter.

exhibited a concentration on one or two tree species: female Hairies on white fir and ponderosa pine, male White-heads on incense cedar, and female White-heads on ponderosa pine (Fig. 1). The distributions of foraging activities among tree species (Fig. 1) were significantly different between seasons for each species-sex sample (χ^2 test, $P < 0.05$), except for male Hairies ($P > 0.05$). During winter, male Hairies increased use of white fir and ponderosa pine, female Hairies increased use of cedar and oak, male White-heads increased use of Douglas fir, and female White-heads showed a pronounced use of incense cedar (Fig. 1). Resource overlap exhibited a decreasing trend during winter for all species-sex samples, except between female Hairies and male White-heads, which had a similar index between seasons (Table 1).

Foraging-substrate use.—All species-sex samples exhibited a concentration of foraging activities on trunks during summer and winter (Fig. 1). Except for female White-heads, all species-sex samples showed an increased use of limbs during winter; twigs were seldom (<5%) used during any season (Fig. 1). The distributions of foraging activities on substrates (Fig. 1) were similar (χ^2 test, $P > 0.1$) between seasons, except for female White-heads ($P < 0.05$). Resource overlap was high for all samples, but dropped during winter between male and fe-

TABLE 2. Foraging height, foraging-tree height and diameter at breast height (dbh), and foraging/tree height ratio.[a] Values are means ± SD; sample sizes are given in the Appendix.

		Hairy Woodpecker		White-headed Woodpecker	
	Season[b]	Male	Female	Male	Female
Foraging height (m)	S	$11.4^{A} \pm 7.33$	$11.6^{A} \pm 5.59$	$10.1^{A} \pm 6.95$	$11.8^{A} \pm 6.65$
	W	$22.1^{*C} \pm 10.44$	$17.0^{*B} \pm 7.80$	$13.9^{*B} \pm 6.66$	$9.7^{A} \pm 8.05$
Tree height (m)	S	$21.1^{B} \pm 10.70$	$20.2^{B} \pm 8.44$	$20.7^{B} \pm 10.43$	$25.8^{A} \pm 10.77$
	W	$31.8^{*C} \pm 10.02$	$26.4^{*B} \pm 9.17$	$28.1^{*B,C} \pm 10.20$	$20.9^{*A} \pm 10.61$
Foraging/tree height ratio[c]	S	0.54	0.57	0.49	0.46
	W	0.69	0.64	0.49	0.46
Tree dbh (cm)	S	$50.5^{A,B} \pm 27.10$	$43.3^{B} \pm 19.97$	$61.1^{A} \pm 31.52$	$54.2^{A,B} \pm 25.84$
	W	$43.0^{A} \pm 27.78$	$47.4^{A,B} \pm 26.70$	$56.8^{B} \pm 27.37$	$39.4^{*A} \pm 28.01$

[a] Within a season, values with same letter (A, B, C) did not differ significantly ($P > 0.05$) as determined by ANOVA and Duncan's multiple range test. Between seasons (summer vs. winter), an asterisk denotes a significant difference ($P < 0.05$) as determined by a *t*-test.

[b] S = summer, W = winter.

[c] Values were obtained from the means presented in this table.

TABLE 3. Daily distribution of foraging activity (percentage of total observations).

Hours after sunrise	Hairy Woodpecker				White-headed Woodpecker			
	Male		Female		Male		Female	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
1	11.1	13.5	2.5	4.9	7.2	0.0	3.1	0.0
2	12.4	1.9	15.7	4.9	13.6	12.9	7.1	0.0
3	15.3	0.0	14.2	0.0	11.7	40.3	12.0	67.1
4	11.5	0.0	21.1	0.0	14.2	21.0	16.4	7.1
5	14.7	30.8	19.9	17.1	15.5	3.2	22.8	0.0
6	9.7	7.7	6.7	0.0	9.3	3.2	6.4	4.3
7	9.7	3.8	4.6	26.8	6.3	1.6	6.2	1.4
8	7.4	7.7	2.3	36.6	3.8	17.7	6.8	20.0
9	4.4	34.6	6.1	9.8	5.1	0.0	6.0	0.0
10	1.2	—[a]	3.1	—	6.8	—	5.7	—
11	2.6	—	3.8	—	6.6	—	7.5	—

[a] Dusk to sunset; no observations made.

male White-heads and especially between female Hairies and female White-heads (Table 1).

Foraging-substrate condition.—During summer, the two species used substrates with contrasting conditions. Hairies concentrated on dead, and White-heads on live, substrates (Fig. 1). During winter, a more even distribution of activities on living and dead substrates was evident for all except female White-heads, which concentrated activities on living trees. The distributions of foraging activities by tree condition (Fig. 1) were similar between seasons (χ^2 test, $P > 0.1$), except for female White-heads ($P < 0.05$). Resource overlap showed moderate (>0.15) increases in winter between male Hairies and male White-heads, female Hairies and male White-heads, and female Hairies and female White-heads (Table 1).

Tree species–foraging substrate use.—Each species-sex sample showed a concentration of activities on two or three tree species–foraging substrate combinations during both seasons (Appendix). Female Hairies increased use of oak limbs and cedar trunks and decreased use of white-fir and ponderosa-pine trunks during winter. Male White-heads increased use of Douglas-fir limbs and maintained use of cedar trunks during winter. Female White-heads dramatically increased use of cedar trunks during winter (74% winter use vs. 13% summer use); no other tree species-substrate combination was used for >7% of foraging activities during winter (Appendix). Male Hairies increased use of white-fir limbs and trunks, as well as ponderosa-pine trunks, and decreased use of Douglas-fir and oak trunks in winter. The distributions of foraging activities by tree species-substrate categories (Appendix) were similar (χ^2 test, $P > 0.1$) for male and female Hairies, but significant for male ($P < 0.05$) and female ($P < 0.001$) White-heads. Resource overlap decreased during winter for all samples except between female Hairies and male White-heads, which showed a slight (0.10) increase (Table 1). The decrease in overlap was rather substantial (about 0.20) between male Hairies and female White-heads and between male and female White-heads, primarily a result of the concentrated use of cedar trunks by female White-heads during winter.

Time of foraging activities.—All species-sex samples concentrated foraging activities during the first 5 h after sunrise during summer (Table 3); foraging times were correlated significantly except between male Hairies and fe-

TABLE 4. Correlations (r_s) of time of day of foraging activities during summer (below diagonal) and winter (above diagonal).[a] $n = 11$ daily time periods for summer, 9 for winter. Original data are given in Table 3.

	Hairy Woodpecker		White-headed Woodpecker	
	Male	Female	Male	Female
Hairy Woodpecker				
Male	—	0.49	−0.78*	−0.64
Female	0.67*	—	−0.36	−0.25
White-headed Woodpecker				
Male	0.76**	0.81**	—	0.77*
Female	0.58	0.71*	0.61*	—

[a] * = $P < 0.05$, ** = $P < 0.01$.

male White-heads (Table 4). During winter, however, foraging activities of male and female Hairies were concentrated 5–9 h after sunrise. Foraging times for male and female White-heads occurred primarily 3–4 h after sunrise, although a minor increase in activity occurred about 8 h after sunrise (Table 3). Correlation analysis showed that winter foraging times of male Hairies and male White-heads were significantly negative, and three of the remaining relationships were negative but not significant. Activity periods of male and female White-heads and of male and female Hairies were positively related, although only the former was significant (Table 4).

Morphological relationships.—All species-sex samples overlapped in body mass, although male Hairies ($\bar{x} = 70$ g) are about 10% heavier than female Hairies and male White-heads (both about 63 g), and about 15% heavier than female White-heads (about 59 g; data from Dunning 1984). Bill length followed a similar pattern: male Hairies ($\bar{x} = 33.3$ mm, SD = 1.06) had the longest bills, followed by female Hairies (30.2, 1.19), male White-heads (28.7, 1.03), and female White-heads (27.1, 0.86). Bill length differed significantly among all species-sex samples as determined by analysis of variance ($P < 0.001$) and Duncan's multiple range test ($P < 0.05$) (see also Short 1982: 319, 328 for size comparisons).

DISCUSSION

A general trend toward decreased overlap in use of foraging sites by Hairy and White-headed woodpeckers during winter was primarily a reflection of the concentration of activities on the trunks of live incense cedar by female White-heads. Except for male Hairies, the others also increased use of cedar during winter. Morrison et al. (1985) documented the increased use of live cedar in winter by many other bird species that winter in Blodgett Forest. Analysis of food availability revealed the presence of a scale insect, *Xylococculus macrocarpae*, under the loose, flaky bark of cedar, the most abundant tree species at Blodgett. Even small-billed species, such as kinglets (*Regulus* spp.) and chickadees (*Parus* spp.), were able to use this seemingly abundant food source. Few insects are available on the bark or foliage surface of any tree species during winter at Blodgett (unpubl. data).

Differential use of cedar by woodpeckers may be related to the ability to extract prey as a function of bill morphology. Smaller-billed female Hairies may be unable, relative to the larger-billed male Hairies, to obtain prey by drilling deep into wood for overwintering insects. Kilham (1970: table 4) also noted that female Hairies foraged superficially by scaling bark in contrast to the deep excavations into wood performed by male Hairies. Male White-heads, possessing roughly the same bill size as female Hairies, also used cedar during both winter and summer. Female White-heads, the smallest among the four species-sex samples examined, spent about 75% of their foraging time on cedar. In southern California, male and female White-heads separated in foraging locations on Coulter pine (*Pinus coulteri*), with males concentrating on the trunks and large cones (Hilkevitch 1974). Males were able to feed on the cones of Coulter pine because of their larger bill relative to females. Otvos and Stark (1985) analyzed the stomach contents of woodpeckers at several locations in California, including Blodgett Forest, during the 1960's. They found that females of both species fed on beetles that inhabited the upper stems of trees, where bark was thin. Stomach analyses revealed that *X. macrocarpae* comprised the second-largest portion of the diet in both sexes of the White-headed Woodpecker: 15% in males and 19% in females. For Hairies, *X. macrocarpae* comprised only 2% of the diet in males and 7% in females. Thus, the occurrence of scale insects in the diet of these woodpeckers agrees with the trend expected from a consideration of bill size (e.g. female White-heads, with the smallest bill, had the greatest percentage of scale insects in their diet).

In the eastern United States, smaller-billed woodpeckers forage more intensively on thin-barked trees in winter than do larger-billed woodpeckers (Kilham 1970, Travis 1977, Conner 1981; see also Morrison et al. 1985). The availability of insects that overwinter under the bark of thin-barked trees was given as the reason smaller birds use this resource. This does not explain why larger-billed birds did not exploit this abundant food resource, especially given the small difference in bill size for the species analyzed in our study. Prey, other than that available on cedar, may be readily available to these woodpeckers (such as prey occurring in tree cambium). But these prey were not sampled at Blodgett. A decrease in niche overlap during winter would be predicted if resources were limiting and species were segregating foraging activities in response to this limitation. Although not measured, resources apparently were not limiting during our study. Changes in foraging behavior during winter appeared to be in response to readily available prey on cedar and not because of interspecific competition for resources. Resource availability—including difficult-to-measure prey found beneath bark and in the cambium—would be a useful addition to further studies of these birds.

Northern and southern populations of White-headed Woodpeckers have been classified as separate subspecies (A.O.U. 1957) based on morphological differences (Grinnell 1902). In the southern part of its range (i.e. southern California), White-heads apparently concentrate activities in pines, often feeding heavily on pine seeds (Bent 1939, Koch et al. 1970, Short 1971, Hilkevitch 1974, K. L. Garrett pers. comm.). Ligon (1973) noted similar feeding by "northern" White-heads in a ponderosa pine forest in Idaho. We did not find a concentration of foraging activities on pines by White-heads. Likewise, Otvos and Stark (1985) reported that pine seeds formed a small part of this species' diet, with most use confined to the fall. Thus, there is apparently a difference in habitat use throughout the range of White-headed Woodpeckers. Sparse use of pine at Blodgett may reflect the mix of tree species there compared with the more monotypic stands of conifer species outside the mixed-conifer zone. Ligon (1973) attributed the lack of difference in foraging behavior between male and female White-heads in Idaho to habitat homogeneity and a lack of diverse food resources.

Times of foraging activities were similar for all species-sex samples in summer. The similarity of foraging times during breeding probably reflects the similarity in requirements both sexes have because of nesting activities. During winter, however, foraging times of male Hairies and male White-heads showed a significant negative relationship. The foraging times of male and female White-heads remained positively related during winter. Given the observed differences in tree species–foraging substrate use, and that male Hairies and male White-heads foraged at different heights, it is unlikely that the differences in foraging times were related to interspecific interactions (here, competition for resources). We do not know if physiological differences between the species or sexes affected the activity periods of the birds. Although winter data are not sufficient for analysis, count data indicated that no negative relationship existed between numbers (index of abundance) of Hairy and White-headed woodpeckers (competition for space) in summer 1983–1985 (unpubl. data).

Although no negative relationships were observed among any of the woodpeckers in terms of abundance or time of foraging activities at Blodgett, the potential for such interactions exists in times of resource limitations (e.g. Wiens 1977). Further, some or most of the woodpeckers overwintering at Blodgett may not be the same individuals that breed there, as some downslope movement during winter is possible (Grinnell and Miller 1944). Therefore, while our analyses do not assign a strong role to interspecific interactions in shaping patterns of resource use between Hairy and White-headed woodpeckers, such a role cannot be ignored. Hairy and White-headed woodpeckers may interact when foraging on pine cones (Ligon 1973). Based on limited observations, Ligon suggested that male White-heads were dominant over female Hairies. The potential for interspecific interactions at a specific food source thus exists, especially during winter if prey are scarce (Ligon 1973). In contrast, Hilkevitch (1974) noted virtually no interspecific interactions between White-heads and other woodpeckers, including Hairies. Further, Short (1982: 323) observed interspecific territory overlap during breeding. Short (1971) postulated that the White-headed Woodpecker evolved in the Pacific Northwest from an ancestor similar to that from which the Hairy Woodpecker evolved. He suggested that the White-headed Woodpecker became restricted in range as the Hairy Woodpecker became sympatric with it. Our results indicate that although within-habitat adjustments in behavior may be evident between these two species, the gross distribution of the two is related primarily to factors other than interspecific interactions (e.g. habitat complexity). Evaluation of resource use between these species in areas of allopatry, and especially experimental manipulations of habitat and prey, would help clarify this question.

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Appendix. Percentage use of 15 substrate-tree species categories used to forage.

	Hairy Woodpecker				White-headed Woodpecker			
Substrate and tree species	Male		Female		Male		Female	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Limb								
Incense cedar	5.0	0.0	6.3	7.3	5.5	1.6	6.7	7.1
White fir	2.5	11.5	4.2	4.9	0.0	0.0	3.3	0.0
Sugar pine	0.0	1.9	0.0	0.0	3.6	1.6	5.0	0.0
Ponderosa pine	2.5	1.9	4.2	0.0	7.3	1.6	5.0	0.0
Douglas fir	5.0	0.0	4.2	0.0	0.0	24.2	6.7	0.0
Black oak	2.5	9.6	6.3	19.5	3.6	3.2	1.7	0.0
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trunk								
Incense cedar	5.0	5.8	8.3	22.0	27.3	22.6	13.3	74.3
White fir	17.5	23.1	22.9	12.2	10.9	3.2	1.7	4.3
Sugar pine	5.0	7.7	2.1	4.9	9.1	8.1	15.0	5.7
Ponderosa pine	17.5	26.9	27.1	12.2	10.9	14.5	31.7	0.0
Douglas fir	17.5	3.8	0.0	2.4	3.6	9.7	3.3	2.9
Black oak	12.5	0.0	4.2	4.9	7.3	8.1	5.0	0.0
Other	5.0	7.7	10.4	7.3	0.0	1.6	0.0	5.7
Other	2.5	0.0	0.0	2.4	10.9	0.0	1.7	0.0
n of individuals	40	60	48	48	55	83	60	81