FORAGING BEHAVIOR OF BARK-FORAGING BIRDS IN THE SIERRA NEVADA

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Data on foraging behavior are often used for examining use of habitat and describing community structure among co-occurring species of birds using the same resource base (e.g., Johnson 1966, Eckhardt 1979, Rusteholz 1981). Differences in tree species, foliage morphology, and bark structure may influence the types of prey taken and the species of bird using the substrate (e.g., Jackson 1979, Holmes and Robinson 1981, Robinson and Holmes 1984). Elucidation of foraging behaviors and tree species preferences is important if we are to determine the role of birds in forest ecosystems, and make informed decisions regarding management of these forests. In this study we describe the use of tree species, foraging modes, and foraging substrates by a group (or "guild," sensu Root 1967) of bark-foraging birds breeding in the western Sierra Nevada. A similar study on foliage insectivores was conducted previously near our study area (see Airola and Barrett 1985).

The species analyzed, in order of decreasing abundance, were: Red-breasted Nuthatch (Sitta canadensis), Brown Creeper (Certhia americana), Red-breasted Sapsucker (Sphyrapicus ruber), White-headed Woodpecker (Picoides albolarvatus), Hairy Woodpecker (P. villosus), and Pileated Woodpecker (Dryocopus pileatus) (see Morrison et al. 1986). All are typical inhabitants of coniferous forests in the Sierra Nevada (Grinnell and Miller 1944). The Downy Woodpecker (Picoides pubescens) and Northern Flicker (Colaptes auratus) occurred rarely in our study area and are not analyzed herein.

STUDY AREA

The study area was the Blodgett Forest Research Station of the University of California-Berkeley, El Dorado County, California. This 1,200-ha forest is located in the mixed-conifer zone (see Griffin and Critchfield 1972) at about 1350 m elevation in the central-western Sierra Nevada. The forest consisted of five predominant conifer species: incense cedar (Calocedrus decurrens; 25% of total basal area, unpubl. data); white fir (Abies concolor, 21%); ponderosa pine (Pinus ponderosa, 19%); sugar pine (P. lambertiana, 10%); and Douglas-fir (Pseudotsuga menziesii, 15%); and one deciduous species, California black oak (Quercus kelloggii, 8%). The forest has been divided into 5- to 37-ha compartments to be managed under various silvicultural systems and is now mostly mature (>70 years old) conifer that is at or near rotation (cutting) age.

During 1983 and 1984 we selected 24 compartments (of mature conifer); compartments totalled about 420 ha (range = 7-37 ha). During 1985 we selected nine compartments, seven of which differed from those used during 1983 and 1984; the 1985 compartments totalled 210 ha (range = 15-37 ha). Selection was not completely randomized because forest silvicultural plans often determined which compartments were available for use. In most cases compartments were not adjacent to each other.

METHODS

About 1250 person-hr were spent observing foraging behavior during the summers (May to mid-July) of 1983 to 1985. We tried to collect data for all species at an equal rate throughout each summer to lessen the influence of possible temporal variation in behavior among species. Observers systematically walked through a compartment recording data on birds as encountered. Only one individual of a species was observed at a particular place and time to avoid the po-
FIGURE 1. Use (%) of tree species (upper bar), foraging modes (middle bar), and foraging substrates (lower bar) for birds at Blodgett Forest during the summers of 1983 to 1985.

We defined the following foraging motions: glean—prey taken from the surface of the substrate while the bird was perched; hover-glean—prey taken from the surface of the substrate while the bird was flying; sallying (hawk, flycatch)—bird leaves a perch, attempts to catch flying prey on the wing, and returns to a perch (see also Eckhardt 1979); probe—prey taken from an opening, such as bark crevices; and peck—bill forcefully struck at the surface. Other foraging motions (e.g., flush-pursuit, aerial flight, chase) were used little and are reported here as a combined “other” category. Flaking of bark was noted primarily during winter at Blodgett Forest (see Morrison et al. 1985), and was not included as a separate category herein.

Data for males and females were combined for this analysis. Although intersexual differences in foraging behavior are known for many woodpeckers (e.g., Kilham 1965, Grubb 1975, Williams 1980), we combined sexes because: (1) we only had marginally enough data for intersexual comparisons in two of the woodpecker species; and (2) we could not usually differentiate sex in the nonwoodpecker species. Except for the Pileated Woodpecker, our sample sizes greatly exceeded those necessary for analysis of avian foraging behavior (i.e., observations on >35 individuals; Morrison 1984). The distribution of foraging activities for use of tree species, modes, and substrates were examined separately for each bird species by chi-square analysis. All data were analyzed using SPSSX (SPSS 1983).

RESULTS

In the results that follow, the distribution of foraging activities for each bird species for use of tree species, and foraging modes and substrates, were significantly different (chi-square analysis, P < 0.05) except as noted.

Differences were evident in the percent use of different tree species by birds; all distributions were significantly different except for the Pileated Woodpecker, which used all tree species with roughly equal frequency. All species except the White-headed Woodpecker and (to a lesser extent) the Brown Creeper demonstrated high use of white fir, and all species except the Red-breasted Sapsucker showed high use of ponderosa pine (Fig. 1). Relative to the other species, the Pileated Woodpecker occurred more on oak, and the

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>x</th>
<th>SD</th>
<th>x</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-breasted Sapsucker</td>
<td>91</td>
<td>11.5</td>
<td>6.63C</td>
<td>41.8</td>
<td>23.55C</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td>89</td>
<td>10.6</td>
<td>6.68C</td>
<td>44.5</td>
<td>24.30C</td>
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<tr>
<td>White-headed Woodpecker</td>
<td>116</td>
<td>11.6</td>
<td>6.59C</td>
<td>58.9</td>
<td>27.36B</td>
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<td>Pileated Woodpecker</td>
<td>48</td>
<td>17.4</td>
<td>8.99A</td>
<td>90.0</td>
<td>42.72A</td>
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<tr>
<td>Red-breasted Nuthatch</td>
<td>126</td>
<td>13.9</td>
<td>6.49B</td>
<td>47.7</td>
<td>22.63C</td>
</tr>
<tr>
<td>Brown Creeper</td>
<td>123</td>
<td>6.7</td>
<td>4.46D</td>
<td>47.9</td>
<td>25.64C</td>
</tr>
</tbody>
</table>

* Sample sizes = number of individuals observed.
TABLE 2. Vigor of foraging trees and foraging substrates used by birds at Blodgett Forest during the summers of 1983 to 1985. Sample sizes in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Foraging tree (%)</th>
<th>Foraging substrate (%)</th>
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<tr>
<td></td>
<td>Alive</td>
<td>Dead</td>
</tr>
<tr>
<td>Red-breasted Sapsucker</td>
<td>76.4</td>
<td>23.6</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td>46.6</td>
<td>53.4</td>
</tr>
<tr>
<td>White-headed Woodpecker</td>
<td>81.1</td>
<td>18.9</td>
</tr>
<tr>
<td>Pileated Woodpecker</td>
<td>55.3</td>
<td>44.7</td>
</tr>
<tr>
<td>Red-breasted Nuthatch</td>
<td>82.8</td>
<td>17.2</td>
</tr>
<tr>
<td>Brown Creeper</td>
<td>86.2</td>
<td>13.8</td>
</tr>
</tbody>
</table>

White-headed Woodpecker and creeper were unique in exhibiting a greater use of incense cedar. In addition, the White-headed Woodpecker had a higher use of sugar pine than the other species.

Only the sapsucker and nuthatch were observed fly-catching. The creeper foraged primarily by gleaning and probing. The nuthatch gleaned extensively, but spent roughly equal time probing and pecking. In contrast to the other woodpeckers, the sapsucker spent similar amounts of time pecking and gleaning. The other woodpeckers pecked and probed >70% of the time (Fig. 1).

All species except the nuthatch concentrated foraging activities on trunks (Fig. 1). The nuthatch used a wide variety of substrates, including twigs and small-sized branches. Although concentrating activities on trunks, the Pileated Woodpecker also showed substantial use of medium-sized branches (Fig. 1).

Pileated Woodpeckers foraged significantly higher than all other species, the nuthatch foraged higher than all remaining species, and the creeper foraged significantly lower than all other species (Table 1). The remaining three species, the White-headed and Hairy woodpeckers, and Red-breasted Sapsucker, had mean foraging heights of about 10 to 11 m.

The Pileated Woodpecker used significantly larger (by fitter at breast height; dbh) trees than all other species; the White-headed Woodpecker used larger trees than the remaining species (Table 1). The average dbh of foraging trees used by the other species was similar (about 42 to 48 cm dbh).

The sapsucker, White-headed Woodpecker, nuthatch, and creeper spent the majority of their time foraging on the live parts of trees (Table 2). The Hairy and Pileated woodpeckers foraged in live and dead trees with similar frequency, but about 70% of their foraging time was on dead substrates (Table 2).

DISCUSSION

Our results indicated that the birds we studied used different combinations of the foraging behaviors examined. All species except the sapsucker showed high use of ponderosa pine; high use of white fir was observed for all except the creeper and White-headed Woodpecker; the white-headed and creeper had higher use of incense cedar, and the white-headed also used more sugar pine than the other species. Where overlap occurred in tree species use (ponderosa pine and white fir), the bird species used different foraging modes and/or other tree species to a greater extent (e.g., compare the Hairy and White-headed woodpeckers). Differences in foraging height, type of substrate used, and tree and substrate vigor also differed among species. For example, although the creeper and nuthatch gleaned extensively (in contrast to most woodpeckers), they foraged at different average heights, and the nuthatch used a wider range of foraging substrates. The sapsucker differed from the other woodpecker species in several ways, most notably in its higher use of gleaning. The use of living substrates by the sapsucker, in contrast to the predominate use of dead wood by other woodpeckers, is likely a reflection of the use of sap as a food source by the sapsucker (see Verner and Boss 1980).

A change in the species or size composition of the forest would likely alter the pattern of resource use by the birds we observed. Such changes are, in fact, underway in the Sierra Nevada due to silvicultural activities (see Morrison et al. 1985). For example, external bark structure changes with tree diameter (e.g., usually becoming thicker and more deeply furrowed with age), which affects prey abundance and the ability of birds to obtain the prey (Jackson 1979, also Morrison et al. 1985). The current trend in the western Sierra Nevada is conversion from mixed-conifer to monotypic stands of ponderosa pine, or mixed stands of ponderosa pine and lesser amounts of Douglas-fir and fir (R. C. Heald, Manager, Blodgett Forest, pers. comm.). Premcommercial- and commercial-thinning activities also remove much of the understory of small, commercially undesirable species or less-vigorous individuals. Although most species in our study used ponderosa pine, they also showed high use of white fir. Further, several species exhibited high use of incense cedar. Although we would predict that conversion to ponderosa pine would probably not eliminate any species we studied, such a change would likely alter the abundance of the birds. The ramifications of such changes on interactions within the bird community, and within the forest ecosystem itself (e.g., bird-insect interactions), are unknown. Our results, as well as those of Airola and Barrett (1985) for foliage insectivores, indicate that efforts should be made to maintain a high diversity of tree species and size classes throughout the mixed-conifer zone of the Sierra Nevada.

This paper elucidates foraging behaviors used by bark foragers during spring and summer. In a related study, Morrison et al. (1986) found a significant increase in the use of incense cedar by many birds during winter. This change was related to prey availability and was
accompanied by changes in foraging mode. Therefore, biologists and resource managers should view the present paper in light of such seasonal changes in behavior. Unfortunately, we did not measure prey availability during the breeding period, a shortcoming that should be eliminated in future studies. Detailed analysis of the surface area of bark available to birds, including limbs and twigs, should also be quantified in the future.

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