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FORAGING ECOLOGY OF BROWN CREEPERS IN A MIXED-CONIFEROUS FOREST

By Kathleen E. Franzreb

Brown Creepers (*Certhia americana*) generally are birds of coniferous and mixed forests. Creepers usually place their nests behind slabs of loose bark associated with older and/or dead trees. General information on nesting chronology is available in Davis (1978). Their diet consists of larvae, pupae, and eggs of insects primarily gleaned from bark crevices; spiders; other small invertebrates; and occasionally seeds (Pearson 1923, Reilly 1968).

Although studies have considered Brown Creeper foraging in winter (e.g., Morse 1970, Willson 1970a,b), little information on foraging behavior during the nesting season is available. Researchers have not focused on the relationship of availability of certain environmental components versus actual use. The purpose of this study was to quantify the foraging ecology of the Brown Creeper with particular emphasis on tree species preferences and tree height use.

STUDY AREA AND METHODS

The study area was located in the Willow Creek watershed, approximately 80 km south of Springerville, in the Apache-Sitgreaves National Forest, Greenlee County, White Mountains, Arizona. Elevations range from 2682 to 2805 m. The watershed supports a mixed-coniferous forest composed predominantly of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and southwestern white pine (*Pinus strobiformis*). A 15.5 ha study plot was established using 9 parallel, flagged transect lines 390 m in length and 50 m apart.

Vegetation analysis.—Vegetation was sampled using the plotless point-quarter method (Cottam and Curtis 1956) whereby 400 trees (with diameter at breast height $\geq$7.6 cm) were measured at 100 points. Importance values (Cottam and Curtis 1956) for each tree species and snags were estimated from the formula: I.V. = relative density + relative dominance + relative frequency. Basal area (m^2/ha) was based on dbh measurements taken during the point-quarter analysis and was used to estimate relative dominance.

Tree height was estimated using a clinometer. Height data were segregated into 9-m height classes and provided frequency data for each height class. Additional details of the methods used in the vegetation analysis are available in Franzreb (1978).

Foraging behavior.—Foraging data on Brown Creepers were obtained from mid-May through August in 1973 and 1974 by systematically walking transect lines. Observations were taken under skies that were clear to less than 30% overcast with wind conditions varying from no wind

to light wind (Beaufort scale 0 to 2). Although data were collected throughout the day, most observations were taken between 0600–1000.

Foraging data were collected for 8 variables: method of prey procurement (glean, hover, hawk, peck/probe—for definitions see Franzreb 1984), stance (standing upright, upside down, or sideways as when on a trunk), foraging substrate (branch/twig, trunk, ground, log), perch diameter, tree species, snag use (by tree species, if possible), tree height, and height of the bird in the tree. One observation per bird per sighting was used to reduce sampling bias.

Niche breadth values were estimated using Levins' (1968) formula whereby $1/B = \sum p_i^2$; where B is foraging niche breadth and p_i is the proportion of observations occurring in the i^{th} resource state. Proportional similarity indices (PSI) (Feinsinger et al. 1981) were calculated for those variables whose resource availability could be quantified (e.g., tree species use, tree height selection). $PSI = 1 - \frac{1}{2} \sum |p_i - q_i|$ where p_i is the proportion of the resource items in state i used by a species, and q_i is the proportion of i items in the resource base available to the birds. The PSI is an indicator of the degree of generalization of a species with respect to a particular foraging variable. Values range from 0 to 1 with lower values indicating greater specialization in that variable.

G-tests (Zar 1974) were used to determine statistical significance of differences between tree species use and availability and for tree height selection versus tree height frequency. Expected values for bird use of particular tree species were estimated from the tree species importance values and also from basal areas. Actual data, not percentages, were used in the tests. The asymptotic variance (V_A) for the proportional similarity index values for tree species based on importance values and tree height were estimated using the "delta method" outlined in Smith (1982). Estimates of niche breadth for the variables were compared using the procedures described by Smith (1982, eq. 18) to determine if niche breadths were similar. Significance levels were defined as $P < 0.05$.

RESULTS

The total tree density was estimated at 626.2 trees/ha. Douglas-fir and ponderosa pine were the dominant tree species. Douglas-fir had the greatest importance value and basal area, and ponderosa pine had the highest average diameter at breast height (dbh) (Table 1). More details of the vegetation analysis are provided in Franzreb (1978) and Franzreb and Ohmart (1978).

Three major patterns of foraging in adult Brown Creepers were noted. Some individuals moved straight up the trunks, carefully detouring around the branches. Others moved up to a branch, went along its undersurface to near the tip—but rarely actually to the tip—and then flew to the top of the branch. From there they moved along the branch top back to the trunk, and then continued up the trunk. Other birds followed a spiral pattern around the trunk as well as the branches as they moved upward. Regardless of which general climbing pattern was

TABLE 1. Vegetation analysis and tree species preferences of Brown Creepers in mixed-coniferous forest, White Mountains, Arizona.

Tree species	No. of obs.	(%)	Tree sp. importance value/3[a,b] (%)	Basal area[c] m²/ha	Average dbh (cm)
Ponderosa Pine (*Pinus ponderosa*)	88	(24.7)	(22.6)	16.3	35.7
Southwestern White Pine (*P. strobiformis*)	39	(11.0)	(15.6)	5.0	20.9
Douglas-fir (*Pseudotsuga menziesii*)	125	(35.2)	(30.6)	17.0	26.4
Alpine Fir (*Abies lasiocarpa*)	0	(0)	(0.5)	0.2	23.0
White Fir (*A. concolor*)	32	(9.0)	(8.1)	4.9	24.8
Blue Spruce (*Picea pungens*)	5	(1.4)	(1.7)	0.3	15.8
Engelmann Spruce (*P. engelmanni*)	17	(4.7)	(4.4)	1.2	21.6
Quaking Aspen (*Populus tremuloides*)	3	(0.9)	(6.7)	2.0	19.9
Snag (dead tree)	47	(13.1)	(9.6)	4.0	22.4
Total	356	(100.0)	(100.0)	50.9	
Proportional similarity index 0.89,[d] 0.89[e]					

[a] Significant difference in use vs availability ($G = 47.3$, $df = 8$, $P < .001$).
[b] Importance value = (relative density + relative dominance + relative frequency).
[c] Significant difference in use vs availability ($G = 43.5$, $df = 8$, $P < .001$).
[d] Based on importance value.
[e] Based on basal area.

used, birds generally worked upward to within 1–3 m of the tree top, and then flew to the trunk of another tree—generally within 1 m of the ground—before repeating the upward process. The point at which an individual vacated one tree for another often coincided with an increase in branch density which probably made it difficult for the bird to maneuver on the trunk.

When comparing creeper use of tree species to basal area, average dbh, or importance value of the individual tree species, it appeared the birds had a slight preference for ponderosa pine, Douglas-fir, and snags (Table 1). Several tree species were used in approximately the proportion in which they occurred in the habitat (e.g., white fir, *Abies concolor*; blue spruce, *Picea pungens*; and Engelmann spruce, *P. engelmanni*). Live aspen was infrequently used, but aspen snags were as popular as any other snag type for foraging sites, comprising approximately 28.9% of overall snag use (Table 2).

Peck-probe was the most commonly used method of prey procurement comprising 92.5% of the observations (n = 329). Gleaning accounted for 6.9% (n = 25) and hawking 0.6% (n = 2) of the observations. Niche breadth was 1.16 for method of prey procurement. Most foraging was categorized as being in the side position (69.3%, n = 247) versus the up (11.3%, n = 40), or down position (19.4%, n = 69). Niche breadth for the stance characteristic was 1.89.

TABLE 2. Use of snags for foraging purposes by Brown Creepers.

Type of snag	No. of observations	Percent
Ponderosa Pine	12	26.7
Douglas-fir	10	22.2
Quaking Aspen	13	28.9
Unidentified	10	22.2
Total	45	100.0
Niche breadth 3.95		

Trunks were the most frequently used foraging substrate (68.7%, n = 245) although foraging on branches was also fairly frequent (30.4%, n = 108) (Table 3). When using branches, creepers generally selected those with the largest diameters (61.3% with diameter ≥5.1 cm) (Table 4).

Approximately 30% of the mature trees on the watershed were ≤9 m in overall height, yet they were used relatively infrequently (16.9%) (Table 5). The tallest trees (>27 m) comprised only 8.2% of the vegetative community but were selected 30.9% by Brown Creepers. Proportional similarity indices were 0.89 and 0.77 for tree species selection and tree height use, respectively, indicating that creepers were significantly more specialized ($Z = 2.02$, $P < 0.05$) in tree height than tree species selection.

When first observed, most creepers were relatively close to the ground. Almost 42% of all observations were of birds within 5 m of the forest floor. Approximately 71.2% of the observations were at or below 10 m.

DISCUSSION

In analyzing the foraging behavior of Brown Creepers and other associated species during the winter and spring in an Illinois woodlot, Willson (1970a) noted a bias toward observing individuals at the lower heights primarily arising because of their increased visibility in such areas. Creepers are normally relatively quiet and inconspicuous in their daily habits. I also found a bias in terms of distance from the ground. However, it is obvious that almost all foraging bouts begin with the bird

TABLE 3. Type of foraging substrate selected by Brown Creepers.

Substrate	No. of observations	Percent
Trunk	245	68.7
Branch/twig	108	30.4
Ground	1	0.3
Log	2	0.6
Total	356	100.0
Niche breadth 1.77		

TABLE 4. Diameter of the branch used by foraging Brown Creepers.

Branch diameter (cm)	No. of observations	Percent
>5.1	55	61.3
>2.5 ≤ 5.1	6	6.5
>1.3 ≤ 2.5	16	17.7
≤1.3	13	14.5
Total	90	100.0
Niche breadth 2.31		

flying down to a low position (usually less than 1 m from the ground) on the trunk. The Eurasian Tree-creeper (*Certhia familiaris*) follows the same basic foraging pattern, spending more than 90% of its foraging time climbing on vertical trunks (Norberg 1979).

Once a bird has proceeded up a tree trunk, what determines when it will switch to another tree? This decision appears to be crucially influenced by the structure and configuration of the tree and the morphological adaptations of the bird. Although quite agile in maneuvering, Brown Creepers tended to change trees when branch density had increased to such a degree that maneuverability may have been impaired.

Numerous morphological adaptations permit the Brown Creeper to effectively forage on the trunk surface. In analyzing ecological morphological adaptations of coniferous forest birds in Sweden and Norway, Norberg (1979) indicated that the Eurasian Tree-creeper was highly adapted for trunk climbing in a vertical head-up position by its long curved claws, long toes, short legs, and long tail for balancing. It is particularly adapted for hovering and slow, maneuverable flight. Although Norberg notes that hovering is not usually associated with the Tree-creeper, occasionally it does hover. Because the Brown Creeper

TABLE 5. Tree height frequency and use by foraging Brown Creepers.

Tree height[a] (m)	Tree height[b] frequency (%)	Number of observations	Percent
≤9	30.0	60	16.9
>9 ≤ 18	38.8	103	28.9
>18 ≤ 27	23.0	83	23.3
>27 ≤ 36	6.5	56	15.7
>36	1.7	54	15.2
Total	100.0	356	100.0
Proportional similarity index 0.77			

[a] Significant difference based on comparison of tree height frequency vs use ($G = 209.3$, $df = 4$, $P < .001$).

[b] Based on measurements obtained during vegetation analysis.

and Tree-creeper have similar ecological requirements and are taxonomically closely related (until recently they were considered conspecifics), morphological adaptations found for the Tree-creeper are also probably applicable to the Brown Creeper.

Brown Creepers were relatively generalized with respect to tree species use as indicated by the high proportional similarity value (0.89) and not as generalized in tree height selection (PSI = 0.77), preferring tall trees. This indicates that, for the species available, the size of a tree seems to be more of a determinant in selection for foraging purposes than the species of tree.

Jackson (1979) noted that interspecific variability in bark surface texture of tree species may affect the abundance of surface arthropods and the ability of foraging birds to use them. The preference of creepers to forage in large ponderosa pine, Douglas-fir, and snags may have been a reflection of the rough bark surface (providing good prey habitat and foraging conditions) and of the large tree size. Taller trees have deeper, more numerous crevices, thus probably more arthropods and insects per unit area. Also, foraging surface will increase exponentially as well as become more diverse as vegetation increases in height (Jackson 1979). Large trees may have been preferred because of the quality of foraging habitat and because more foraging surface was available on such trees as indicated by the higher dbh values and larger and more numerous limbs.

A Brown Creeper using the largest trees would probably increase its foraging efficiency and net energy gain because it would not have to fly from tree to tree as frequently. An increase in foraging surface availability may also account for the preferences of creepers to select the largest branches.

Basal area measurements were considered a reasonably reliable indication of substrate availability for the Brown Creeper because of its predilection for foraging on trunks. Although a comparison of creeper use to importance values indicated a preference for ponderosa pine, a similar comparison to basal area showed that the birds used this species less than expected. Because ponderosa pine had the highest average dbh and was among the tallest of trees, it probably provided more foraging substrate than any other tree species except possibly Douglas-fir. Foraging bouts on large ponderosa pines tended to be prolonged and no doubt reflected the greater availability of foraging substrate. Had foraging time been used instead of point observations, an even stronger selection for ponderosa pine would have been obvious.

No information is available on arthropod or insect abundance, distribution, or availability in this study plot. However, various tree species support different invertebrate faunas (Southwood 1961). Hence, tree species preferences may also reflect the creeper's ability to obtain food.

Foraging behavior of Brown Creepers also may be influenced by interactions with numerous sympatric species foraging on the same trees and in similar portions of the trees. These include the Downy Wood-

pecker (*Picoides pubescens*), Mountain Chickadee (*Parus gambeli*), and Red-breasted (*Sitta canadensis*), White-breasted (*S. carolinensis*), and Pygmy nuthatches (*S. pygmaea*). The strategy employed by the Brown Creeper is to specialize highly in its foraging repertoire. Willson (1970a) found the Brown Creeper to be the most specialized of the species she examined. She noted that although creepers spent a great deal of time on each trunk, they moved continuously, invariably in a forward and upward direction. The results of this breeding season study in mixed-coniferous forest agree with her winter/spring analysis of an Illinois woodlot.

It is not known how behaviorally flexible any given individual is in its foraging behavior, but the overall feeding ecology of this species is quite stereotyped. A certain amount of flexibility provides for a rapid response to different environmental conditions present in any given area for any particular season. This suggestion is supported by Morse's (1970) study of mixed-species foraging flocks of birds in Louisiana, Maine, and Maryland. He found that creepers tended to forage in the peripheral parts of deciduous trees in mixed forest, while showing a greater propensity to use trunks in coniferous forest.

In this study, it may be argued that tree height use is an artifact of another variable that creepers evaluate while foraging, such as dbh. Even if this were so, the information on height selection can still be used by land managing agencies engaged in logging activities to predict the effects of different logging prescriptions on Brown Creepers. The fact that creepers did not use a recently logged (moderately heavy overstory removal) study plot in this same watershed (Franzreb and Ohmart 1978) suggests that they are sensitive to logging practices.

Niche breadth and proportional similarity index values reflect the foraging specialization of this species, particularly in method of foraging, stance, foraging substrate, and perch diameter. Yet the Brown Creeper is fairly diverse in other foraging categories such as tree height and tree species selection. Hence, it appears that while presenting an overall impression of strong stereotypy, the Brown Creeper is fairly adaptable to varying habitat regimes.

SUMMARY

Brown Creeper (*Certhia americana*) foraging ecology was examined during the 1973 and 1974 breeding seasons in a mixed-coniferous forest, White Mountains, Arizona. Gleaning was the primary foraging method and was conducted mainly from a sideways stance position. Brown Creepers selected trunks (68.7%) as the primary foraging sites, although branches were also commonly used (30.4%). Creepers preferred to forage on ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and snags and preferred large trees. Tree species, perch diameter, and tree-height selection reflected the largest foraging surface available. If more surface area is available per tree, fewer flights between trees are necessary, thus the birds conserve energy. The extent of this ad-

vantage would be influenced by the distribution, abundance, and availability of prey. Brown Creepers were relatively generalized in tree species selection (PSI = .89) but were significantly more specialized ($Z = 2.02$, $P < .05$) in tree height use (PSI = .77). This suggested that the height of a tree (and its concomitant surface area available for foraging) seemed to be more of a determinant in substrate selection than was the species of tree. Although stereotyped in many aspects of foraging, the Brown Creeper was relatively behaviorally flexible in tree species and tree height selection.

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