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GEOGRAPHIC VARIATION IN FORAGING ECOLOGIES OF BREEDING AND NONBREEDING BIRDS IN OAK WOODLANDS

WILLIAM M. BLOCK

Abstract. I studied geographic variation in the foraging ecology of four breeding and four nonbreeding species in three oak (*Quercus* spp.) woodlands of California. Variations were evident for all species. Variations in tree-species use, foraging tactics, substrates, and behaviors were species-specific. For example, White-breasted Nuthatches (*Sitta carolinensis*) used tree species with different frequencies at each study area, although they specialized in where and how they foraged within a tree. The foraging behavior of Yellow-rumped Warblers (*Dendroica coronata*) varied little among study areas, although they were generalists in their use of trees and in their foraging locations. Because foraging ecologies of birds can be highly site-specific, studies should be conducted at different locations. To preserve site-specific characteristics of a species' foraging ecology, researchers should not pool samples from different geographic locations.

Key Words: Geographic variation; oak woodlands; foraging ecology; tree-species use; foraging location; foraging behavior.

Because foraging ecologies are strongly influenced by the types and abundances of resources available to birds (e.g., Gibb 1960, Karr 1976, Morse 1980b), different patterns of foraging may occur at different seasons or locations (Morse 1971b, Laurent 1986).

Interpretations of all aspects of avian foraging ecology probably depend on the scale of observation (Allen and Starr 1982, Hurlbert 1984, Wiens et al. 1986b). Results of studies that are restricted to a single location or a single season might apply only to the place or time of study (Wiens et al. 1987b); studies across space and time include greater variation in patterns of resource use and may provide different interpretations. Many studies have related seasonal variations in resource abundance to foraging behaviors (e.g., Austin 1976, Travis 1977, Alatalo 1980, Conner 1981, Hutto 1981b, Wagner 1981b); Arnold (1981) found no studies of geographic variation of foraging by birds, a topic that has been addressed only in recent years (Maurer and Whitmore 1981; Sabo and Holmes 1983; Wiens et al. 1987b; Petit, Petit, and Petit, this volume).

Foraging by birds encompasses three primary aspects of resource use. These are: (1) general characteristics of where foraging occurred (Holmes and Robinson 1981), such as species of plant as well as its size, shape, and vigor; (2) specific characteristics of where the bird foraged in relation to the plant used for foraging (MacArthur 1958, Hutto 1981b), including the relative position of the bird within the canopy, the foraging perch, and the height of the bird; and (3) the behavior of the bird: foraging maneuver (e.g., glean, peck, probe), rate of foraging, and foraging substrate (Root 1967, Morrison 1982).

In this paper, I explore geographic variation in the foraging ecology of several breeding and nonbreeding species found in oak and oak-pine woodlands of California. The study was done along a latitudinal gradient of 580 km. My specific objectives were to compare characteristics of the species of plant where foraging occurred, the location of the bird in relation to the plant, and the foraging behavior of the bird.

STUDY AREAS AND METHODS

All study areas were in oak or oak-pine woodlands; each differed from the others in topography and in the structure and composition of the vegetation.

Sierra Foothill Range Field Station (SF), Yuba County, is in the foothills of the Sierra Nevada, about 25 km northeast of Marysville. Elevation ranged from 200 to 700 m on a general west-northwest facing slope. Blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and digger pine (*Pinus sabiniana*) were the major species of trees with lesser amounts of California black oak (*Q. kelloggii*), valley oak (*Q. lobata*), California buckeye (*Aesculus californicus*), and ponderosa pine (*Pinus ponderosa*). Most stands consisted of mixtures of blue oak, interior live oak, and digger pine, although relatively pure stands of blue or interior live oak were not uncommon. The composition and structure of the canopy and understory had been modified by historic land-use practices. With the exception of 60 ha of fenced areas, the remaining 2500 ha of the Station have been grazed by cattle which has reduced much of the shrub and herbaceous understory. In addition, trees in many stands had been removed, either selectively or completely, as part of range management practices.

San Joaquin Experimental Range (SJ), Madera County, is in the foothills of the Sierra Nevada, about

40 km north of Fresno. Elevation ranged from 200 to 500 m on a generally southwest facing slope. Blue oak, interior live oak, and digger pine were the major tree species and they generally occurred in mixed-species stands. Stands of pure blue oak and blue oak savanna were not uncommon. About 20 ha of SJ were fenced to exclude cattle grazing. Because of shallow soils and a southerly exposure, SJ supported a sparser shrub understory than that found at SF. This understory was further reduced by cattle grazing, resulting in widely scattered stands of mature shrubs.

Tejon Ranch (TR), Kern County, is about 50 km south of Bakersfield in the Tehachapi Mountains. Elevation ranged from 1100 to 1700 m; aspect included all cardinal directions. Major trees found on the ranch included blue oak, valley oak, California black oak, interior live oak, canyon live oak (*Quercus chrysolepis*), Brewer's oak (*Q. garryana* var. *breweri*), and California buckeye. These trees generally occurred in pure stands of single species, with mixes found along narrow ecotones. The terrain of TR was steep and rugged. Consequently, aspect and vegetation changes were distinct, creating a mosaic landscape of various vegetation types. Cattle grazing modified the composition and structure of the shrub and herbaceous layers. Trees were selectively removed as part of a commercial firewood enterprise, which altered the density and size structure of some stands of oaks. Most stands, however, never had any trees removed.

Field Methods

I established about 30 km of transects each at SF and TR. At SJ, I used 40 km of transects previously established by J. Verner for a different study. During the breeding season (April–June 1987) I studied four species of birds that used different modes of foraging: Plain Titmouse (*Parus inornatus*), a foliage- and bark-gleaning generalist; White-breasted Nuthatch (*Sitta carolinensis*), a bark forager; Ash-throated Flycatcher (*Myiarchus cinerascens*), a flycatcher and foliage gleaner; and Western Bluebird (*Sialia mexicana*), a ground forager. During the nonbreeding season (September 1986–February 1987) I studied: Plain Titmouse; White-breasted Nuthatch; Yellow-rumped Warbler (*Dendroica coronata*), a foliage gleaner; and Dark-eyed Junco (*Junco hyemalis*), a ground forager. Three observers collected data during the breeding season, and four in the nonbreeding season. All observers participated in training exercises to standardize the way data were collected. Observers followed the general direction of a transect, staying within 100 m of either side. Once a bird was encountered the observer watched it for 10 s but recorded no data. This allowed the bird to resume "normal" activities after being disturbed and minimized the observer's likelihood of recording only conspicuous activities. During the following 10 s the observer recorded the species, height, diameter, and crown radius of the plant (tree generally) where foraging was observed; the height of the bird and its relative position from the center to the edge of the canopy; foraging and perch substrates (twig [≤1 cm diameter], small branch [1–10 cm diameter], medium branch [10–30 cm diameter], large branch [>30 cm diameter], leaf, ground, air); and the foraging maneuver (search, glean, peck, probe, pluck, flycatch, fly-glean, hover-glean). The location of each foraging sample was marked with plastic flagging and mapped to try to ensure spatial independence of foraging observations for individual species within the same season.

At each study area I used the point-center quarter method (Cottam and Curtis 1956) to sample the relative frequencies, heights, and diameters of the trees occurring there. One hundred points were established at TR and SF using a systematic-random sampling design (Cochran 1977; see Block and Morrison 1987 for the procedures used in point placement). At SJ, I selected 100 points from bird counting stations previously established by Verner. Although I recorded data on the closest tree or shrub within each quarter, I report here only data pertaining to trees.

Data Analysis

Because some of the species used in this analysis were monochromatic, I pooled sexes of all species. Similarly, ages of many of these birds were difficult to distinguish in the field (i.e., adults, first-year hatching birds), so I pooled data from all ages.

Prior to analysis I developed new variables from the original data using simple arithmetic transformations. Relative height was calculated as the activity height of the bird relative to the total height of the plant. Foraging and search rates were defined as the number of foraging or searching motions per unit of time. Foraging and search times were the total number of seconds during each 10 s sample spent foraging and searching, respectively. Foraging and search speeds were the distances moved per unit of time while foraging or searching.

Variables were analyzed differently depending on whether they were continuous or categorical. I used one-way analysis of variance (Sokal and Rohlf 1969: 204) to test for among-area differences of each species' foraging ecology for diameter, height, and crown radius of the foraging plant; relative position of the bird from the crown center and activity height; foraging rate, time, and speed; and search rate, time, and speed. I used log-linear analyses (Fienberg 1980:13) to compare plant species, foraging activities, and perch and foraging substrates of each species at the three study areas.

I also used log-linear analyses to compare relative frequencies of the tree species used by each bird with the relative frequencies of trees occurring at each study area. I used Mann-Whitney U-tests (Conover 1980) to compare the heights and diameters of the trees used by each species with those of the trees present at each area.

RESULTS

Breeding Birds

Tree use

All birds used tree species with different frequencies in comparisons among and within study areas, except Plain Titmice at SF (Fig. 1; likelihood ratio chi-squares, $P < 0.05$). White-breasted Nuthatches and Western Bluebirds, however, appeared to use blue oaks more frequently than they occurred at each study area (Fig. 1). Both the nuthatch and titmouse exhibited significant

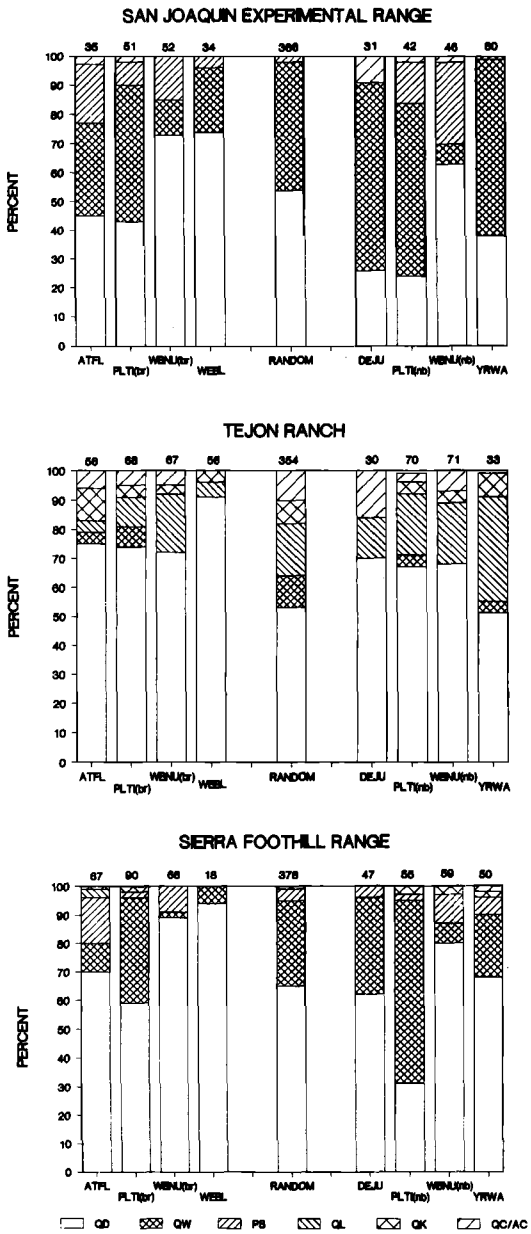

FIGURE 1. Relative frequencies of tree species used by and available to Ash-throated Flycatchers (ATFL), Plain Titmice (PLTI), White-breasted Nuthatches (WBNU), Western Bluebirds (WEBL), Dark-eyed Juncos (DEJU), and Yellow-rumped Warblers (YRWA) in oak woodland habitats in California from September 1986 to February 1987 and March to June 1987. Tree codes are blue oak (QD), interior live oak (QW), digger pine (PS), valley oak (QL), California black oak (QK), and other (OT). Not all bars total 100% because rare categories were not included. Sample sizes are presented on the top of the bars.

TABLE 1. SUMMARY OF COMPARISONS AMONG STUDY AREAS FOR CONTINUOUS VARIABLES OF THE FORAGING ECOLOGIES OF FOUR SPECIES OF BREEDING BIRDS FOUND IN OAK WOODLANDS OF CALIFORNIA FROM MARCH–JUNE 1987

Variable	Ash-throated Flycatcher (58, 42, 71)[a]	Plain Titmouse (69, 55, 92)	White-breasted Nuthatch (67, 52, 66)	Western Bluebird (56, 35, 18)
Tree characteristics				
Diameter		**[b]	**	*
Height	*	**	**	
Crown		*	**	
Foraging location				
Crown position		**	**	
Activity height	*		**	**
Relative height		**	**	**
Foraging behavior				
Foraging rate	**			**
Foraging time	*	**	*	**
Foraging speed	*			**
Search rate		**		
Search time		**		
Search speed				

[a] Number of foraging samples from TR, SJ, and SF, respectively.
[b] One-way analysis of variance: * $P < 0.05$; ** $P < 0.01$.

geographic differences for the heights, diameters, and crowns of the trees (Table 1). In contrast, Ash-throated Flycatchers were consistent in their use of diameters and crowns, and Western Bluebirds consistently used trees of a similar height and crown. There were no significant differences in the diameters of the trees used by Plain Titmice at TR compared to the size of the trees present, nor were there any significant differences in the heights of trees used by titmice at TR and SJ (Mann-Whitney U-tests, $P > 0.05$). The heights of trees used by Ash-throated Flycatchers and Western Bluebirds were similar to their occurrences at TR and SJ, and also for the White-breasted Nuthatch at TR (Mann-Whitney U-tests, $P > 0.05$).

Activity location

Plain Titmice and White-breasted Nuthatches exhibited geographic variation in foraging locations within the tree canopy. The foraging height of the Plain Titmouse was consistent among study areas, but its relative foraging height varied, as did that of the nuthatch and bluebird (Table 1). Geographic variation in the use of foraging perches occurred for all four species (Fig. 2; likelihood ratio chi-squares, $P < 0.05$).

Foraging behavior

Foraging activities and foraging substrates differed among areas for all four species (Fig. 2;

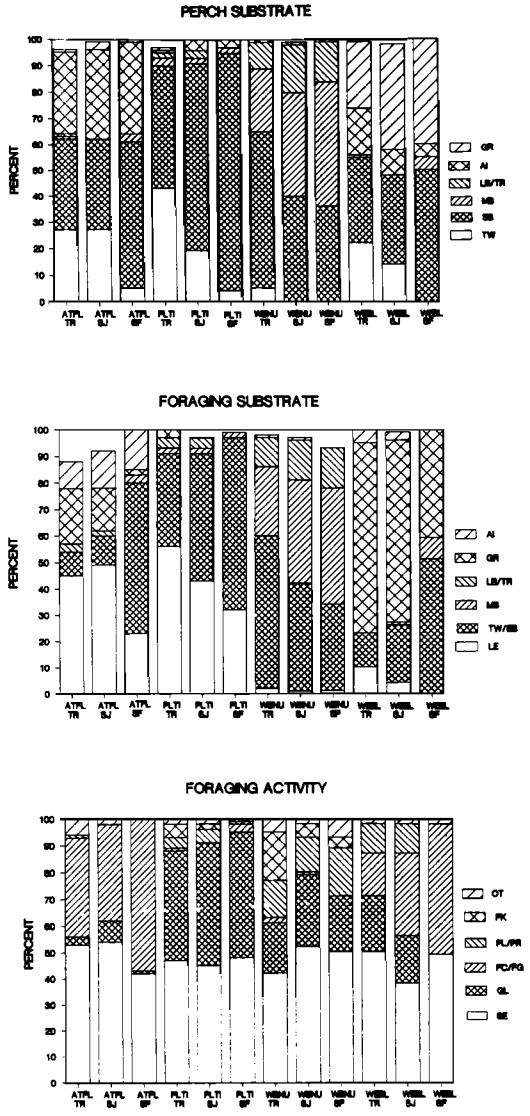

FIGURE 2. Relative frequencies of breeding bird use of perch substrates, foraging activities, and foraging substrates by four species at three oak woodland habitats in California from March to June 1987. Species codes are given in Figure 1, area codes are given in the text. Codes for perch and foraging substrates are leaf (LE), twig (TW), small branch (SB), medium branch (MB), large branch (LB), trunk (TR), ground (GR), and air (AI). Codes for foraging activities are search (SE), glean (GL), flycatch (FL), fly-glean (FG), pluck (PL), probe (PR), peck (PK) and other (OT). Not all bars total 100% because rare categories were not included. Sample sizes are given in Table 1.

likelihood ratio chi-squares, $P < 0.05$). White-breasted Nuthatches, however, foraged consistently on bark, regardless of location. Depending on the study area, Ash-throated Flycatchers and

TABLE 2. SUMMARY OF COMPARISONS AMONG STUDY AREAS FOR CONTINUOUS VARIABLES OF THE FORAGING ECOLOGIES OF FOUR SPECIES OF NONBREEDING BIRDS FOUND IN OAK WOODLANDS OF CALIFORNIA FROM SEPTEMBER 1986–FEBRUARY 1987

Variable	Dark-eyed Junco (30, 43, 49)[a]	Plain Titmouse (71, 46, 60)	White-breasted Nuthatch (71, 46, 59)	Yellow-rumped Warbler (33, 85, 51)
Tree characteristics				
Diameter	*[b]	**		
Height	**	**	**	*
Crown	*	*		
Foraging location				
Crown position	**	**		**
Activity height				*
Relative height	*	**		**
Foraging behavior				
Foraging rate			**	
Foraging time	**	**	**	**
Foraging speed	**	*		
Search rate	**			
Search time	**			
Search speed	*	**		*

[a] Number of foraging samples from TR, SJ, and SF, respectively.
[b] One-way analysis of variance: * $P < 0.05$; ** $P < 0.01$.

Western Bluebirds foraged at different rates, speeds, and durations. Foraging time differed among areas for both the titmouse and nuthatch, and the titmouse searched at different rates and for different periods of time at each study area.

NONBREEDING BIRDS

Tree use

All birds generally used tree species with different frequencies among and within study areas (Fig. 1; likelihood ratio chi-squares, $P < 0.05$). Plain Titmice used trees in proportion to their occurrence at TR and Dark-eyed Juncos did so at TR and SJ (likelihood ratio chi-squares, $P > 0.05$). The trees used by Plain Titmice and Dark-eyed Juncos also differed among areas in diameter, height, and crown radius (Table 2). The heights of trees used by White-breasted Nuthatches and Yellow-rumped Warblers differed among study areas (Table 2). The diameters of trees used by each bird differed from those present at each study area in all comparisons, except for titmice at TR (Mann-Whitney U-tests, $P < 0.05$). The heights of trees used by titmice, juncos, and warblers were similar to those present at TR and SJ, and similarly for nuthatches at TR (Mann-Whitney U-tests, $P > 0.05$).

Activity location

The use of foraging perches differed among study areas for all birds (Fig. 3; likelihood ratio

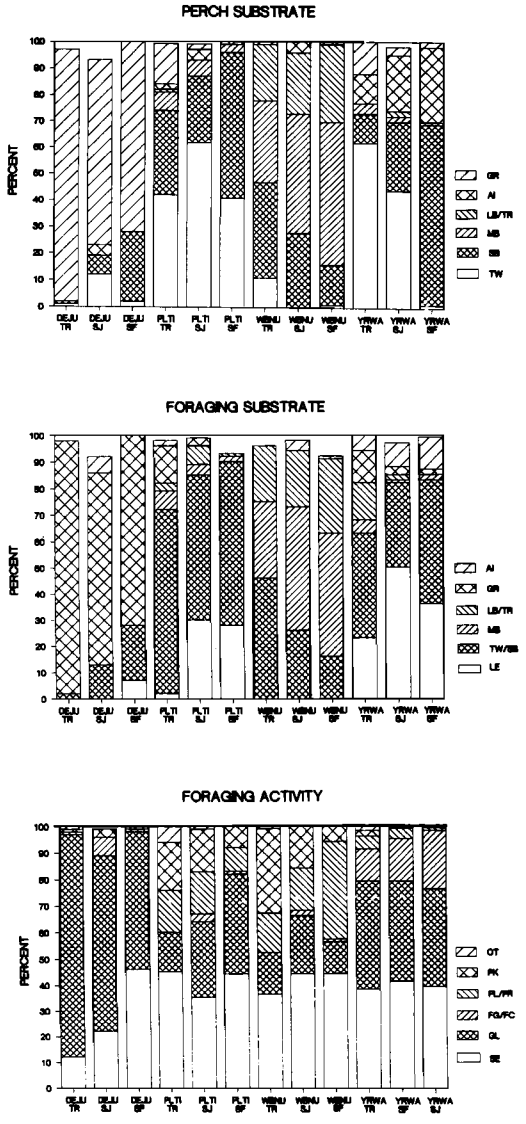

FIGURE 3. Relative frequencies of nonbreeding bird use of perch substrates, foraging activities, and foraging substrates by four species at three oak woodland habitats in California from September 1986 to February 1987. Species codes are given in Figure 1, area codes are given in the text. Substrate and activity codes are given in Figure 2. Not all bars total 100% because rare categories were not included. Sample sizes are given in Table 2.

chi-squares, $P < 0.05$). Dark-eyed Juncos, Plain Titmice, and Yellow-rumped Warblers foraged at different positions in the canopy, and at different relative heights. Activity heights for the warbler differed among study areas (Table 2).

Foraging behavior

All birds but the Yellow-rumped Warbler showed geographic variation in foraging activities (Fig. 3; likelihood ratio chi-squares, $P < 0.05$). Foraging substrates used by warblers, however, differed among study areas, as did those used by juncos, nuthatches, and titmice (Fig 3; likelihood ratio chi-squares, $P < 0.05$). Dark-eyed Juncos foraged at a different speed and for a different duration, and they searched at different rates, speeds, and durations at each study area. Foraging times also differed for the Plain Titmouse, White-breasted Nuthatch, and the Yellow-rumped Warbler. Titmice searched and foraged, and warblers searched, at different speeds at the study areas. Nuthatches foraged at different rates among areas (Table 2).

DISCUSSION

I found geographic variation in all aspects of the foraging ecologies of both breeding and nonbreeding birds in California oak woodlands. The types and magnitudes of this variation appeared to be species-specific, as species exhibited variation differently for tree use, foraging location, and foraging behavior. This agrees with and extends studies during the breeding season (e.g., Maurer and Whitmore 1981, Sabo and Holmes 1983, Wiens et al. 1987b) to the nonbreeding season.

Wiens et al. (1987b) attributed variations in foraging behaviors to differences in local environmental conditions. The vegetation at each of my study areas was unique in structure and composition. Consequently, the types and dispersion of suitable foraging patches, biotic pressures, such as competition and predation (Wiens 1977, Ekman 1986), and weather (e.g., see Grubb 1975) all probably interacted to influence local patterns of foraging.

Studies restricted to one location probably provide little insight into the type or magnitude of a species' plasticity. By contrast, studies that pool data across areas may include too much variation and, subsequently, the results may conceal site-specific behaviors. Investigators should not extend results from one location to different locations or base analyses on data pooled from geographically distinct areas.

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