

*Interspecific, Spatial, and Temporal Variation*

WITHIN-SEASON AND YEARLY VARIATIONS IN AVIAN FORAGING LOCATIONS

SALLIE J. HEJL AND JARED VERNER

*Abstract.* We studied monthly and yearly differences in the foraging sites and substrates of Plain Titmice (*Parus inornatus*) and Bushtits (*Psaltriparus minimus*) in a foothill oak-pine woodland in the central Sierra Nevada during the breeding seasons of 1979 and 1980. The greatest intraspecific differences observed for both species were monthly changes in the use of foraging sites (primarily plant species) and substrates (plant part to which the foraging maneuver was directed) and yearly differences in foraging substrates. The main interspecific differences were in foraging sites used overall and in monthly usages of substrates. Several patterns of resource use paralleled phenological changes in the plant species upon which the birds foraged. For example, both species foraged more on buckbrush (*Ceanothus cuneatus*) during the flowering stage, and Plain Titmice foraged more on blue oak (*Quercus douglasii*) as new leaves reached full growth. Pooling data across months in the same breeding season would have hidden these variations. Furthermore, ignoring site-substrate interactions makes it difficult to interpret patterns in avian foraging.

*Key Words:* Foraging; within-season variation; yearly variation; Plain Titmouse; Bushtit; oak-pine woodlands; California.

Researchers have commonly pooled observations of avian foraging behaviors within seasons and across years (James 1976, Holmes et al. 1979b, Holmes 1980, Conner 1981, Holmes and Robinson 1981, Morrison 1981, Lewke 1982, Franzreb 1983a, Airola and Barrett 1985, Morrison et al. 1985). Seasonal differences in foraging behavior have often been acknowledged (Conner 1981, Lewke 1982, Morrison et al. 1985), but within-season and yearly differences usually have not, in spite of the fact that such differences are reflected in diets (Holmes 1966, Root 1967, Busby and Sealy 1979, Rotenberry 1980a) and behaviors of birds (Holmes 1966; Root 1967; Busby and Sealy 1979; Alatalo 1980; Wagner 1981b; Ford, Huddy, and Bell, this volume; Sakai and Noon, this volume; Szaro et al., this volume). Pooling heterogeneous data sets in this manner could obscure important short- and long-term differences in avian foraging and lead to incorrect interpretations of ecological relationships.

Within-season and yearly differences in diets and foraging behaviors have been demonstrated in many habitats. In five seasons near Barrow, Alaska, Holmes (1966) documented within-season and yearly changes in prey availability and in the associated foraging behavior and diet of Dunlins (*Calidris alpina*). Root (1967) recorded seasonal and yearly differences in prey availability and in the associated diet of Blue-gray Gnatcatchers (*Poliophtila caerulea*) in a coastal oak woodland in California. Both the sandpiper and the gnatcatcher also selected certain prey types. On the other hand, although Busby and Sealy (1979) found monthly and yearly differ-

ences in the foraging behavior and diet of Yellow Warblers (*Dendroica petechia*) in Manitoba, the warblers consumed prey in proportion to their availability. Alatalo (1980) studied the foraging behaviors of five bird species in coniferous forests in Finland throughout 1 year and for 3 months of another year, observing within- and between-season shifts in their foraging behaviors. Similarly, Rotenberry (1980a) found within-season, between-season, and yearly differences in diets of three ground-foraging passerines in shrubsteppe habitats of southeastern Washington during two breeding seasons and one complete year. Wagner (1981b) documented seasonal and yearly differences in foraging behavior of a foliage- and bark-gleaning guild in a California oak woodland.

We studied the foraging locations of Plain Titmice (*Parus inornatus*) and Bushtits (*Psaltriparus minimus*) in a foothill oak-pine woodland to: (1) discern possible intraspecific variations in foraging locations between years or from month to month in the same year, (2) assess the similarities and differences in foraging locations of the two species during the same time periods, and (3) learn whether monthly and yearly differences in foraging locations of either species reflected observed changes in plant phenology.

STUDY AREA AND METHODS

*Study area.* The study was done during the breeding season of both species at the San Joaquin Experimental Range in March, April, and May during 1979 and 1980. The Range is located approximately 32 km north of Fresno, in Madera Co., California. Elevation ranges

from 215 to 520 m. The climate is one of hot, dry summers and cool, wet winters.

Field observations were made on a 19.8 ha (300 × 660 m) plot gridded at 30-m intervals and situated within approximately 32 ha of foothill woodlands that had not been grazed by cattle or managed in any other significant way since 1934. Vegetation on the plot was mainly oak-pine woodland, with some small patches of blue oak (*Quercus douglasii*) savanna, chaparral, and annual grasslands. Buckbrush (*Ceanothus cuneatus*), with 18.6% crown cover, was the most abundant shrub on the plot. Among the trees, gray pine (*Pinus sabiniana*) had a crown cover of 12.5%, interior live oak (*Q. wislizenii*) had 7.2%, and blue oak had 5.4%. The nine remaining tree and shrub species contributed only 4.5% crown cover.

**Bird observations.** One observer recorded data in 1979 and three did so in 1980; the observer in 1979 also observed in 1980. Observers walked along alternate, numbered lines in the long dimension of the grid. Lines walked and the direction of travel were regularly selected to ensure even coverage of all segments of the grid. Walking and stationary search for birds were alternated approximately every 15 min. Observations were made from sunrise to sunset.

Only certain individuals were selected for observation. To avoid bias toward singing birds, observers did not hunt out singing birds. However, most birds sang or called during the observation period. Only the first bird detected in a flock or pair was used as a subject, as locations of flock or pair members would not be expected to be independent. A new individual was chosen as a subject only if the observer had traveled at least 30 m or at least 10 min had elapsed since the last record of a given species. This constraint was imposed in an attempt to increase independence among samples.

From the time a bird was selected, the observer counted slowly to 5 (approximately 5 s) to give time to assess the bird's activity. Its activity at the count of "5" was recorded as an instantaneous sample. If the bird was obviously searching for food at that instant, observations continued until it executed a distinct foraging maneuver (assumed to indicate an attempt to secure food). Two aspects of the location of the foraging maneuver will be examined in this paper as follows: (1) site (gray pine, blue oak, interior live oak, buckbrush, and other, including all other plants, air and ground); and (2) substrate, the exact part of the plant or environs toward which a foraging maneuver was directed (twig [ $<5$  mm in diameter], small branch [5 mm–10 cm in diameter], large branch [ $>10$  cm in diameter], flower bud, flower, catkin, fruit, leaf bud, leaf, trunk, air, and ground).

**Plant phenology.** Phenology of the major woody plant species was sampled weekly during both years and summarized by 2-week periods. Trees sampled were gray pine, blue oak, interior live oak, and California buckeye (*Aesculus californica*). Shrubs sampled were buckbrush, redberry (*Rhamnus crocea*), California coffeeberry (*R. californica*), mariposa manzanita (*Arctostaphylos mariposa*), bush lupine (*Lupinus albifrons*), poison oak (*Toxicodendron diversilobum*), bush penstemon (*Keckiella breviflora glabrata*), and blue elderberry (*Sambucus mexicana*).

Random samples of 10 shrubs and trees of each species were selected, except for species with fewer than 10 individuals on the plot, in which case all individuals were sampled. Eight branches (two each on the north, east, south, and west sides) were selected on each plant, at approximately breast height, and labeled with small, numbered, metal tags. The phenology of each branch was recorded weekly during both growing seasons. Some branches were grazed during the course of the study; these were replaced with the nearest neighbor. All phenological stages present on a given branch were noted. Vegetative growth was recorded as budding, swollen buds, elongated buds, new leaves, stem elongation, and full-sized leaves. Reproductive phenological states included initial budding, swelling of the bud, opening of the bud, full flowers present, fruits set, fruits developing, fruits developed, catkins emerged, and pollen released when evident.

**Statistical analyses.** Because log-linear models can be used to describe data from a multiway contingency table (Fienberg 1970, 1977; Bishop et al. 1975), we searched for log-linear models that best fit our data. We would have preferred to analyze our data in one comprehensive analysis, since we know that important interactions between foraging site and substrate exist. However, data on foraging sites were analyzed separately from foraging substrates, because our data set was too small to classify each record by site and substrate as well as by year, month, and bird species in a multiway contingency table. (Too many sampling zeros would have occurred. According to our statistical consultant, the total number of observations should be at least four times the number of cells in the contingency table; J. A. Baldwin, pers. comm.) Because birds may use a hierarchical decision-making scheme in which they first choose a site and then a substrate within that site (an extension of the habitat selection ideas of Hutto [1985a]), we thought it reasonable to analyze site and substrate separately.

To find the best model for foraging site, we categorized each record into four variables: (1) bird species, (2) year, (3) month (= March [the first two phenological periods], April [the second two phenological periods], or May [the last two phenological periods]), and (4) site. The result was a  $2 \times 2 \times 3 \times 5$  contingency table. To find the best model for foraging substrate, we pooled across foraging sites. We categorized each record by bird species, year, month, and foraging substrate for the second model. The month variables were defined as above. Foraging substrate included four categories: (1) bark surface (= twig, small branch, large branch, or trunk), (2) foliage (= leaf or leaf bud), (3) reproductive parts (= flower bud, flower, catkin, or fruit), and (4) other (= air or ground). The result was a  $2 \times 2 \times 3 \times 4$  contingency table. Foraging site and foraging substrate were treated as response variables in the chosen models. The biological relevance of the interactions entering the models, which included foraging site and foraging substrate, are discussed later. Other interactions that entered models indicated sampling differences; these interactions are discussed in less detail.

We chose a model based on three criteria. Initially, we determined which models had P-values that were close to but greater than 0.05. From those models, we then chose the simplest ones (those with fewer and

TABLE 1. THE CHOSEN LOG-LINEAR MODELS FOR FORAGING SITE AND FORAGING SUBSTRATE. SAMPLE SIZES FOR PLAIN TITMICE WERE 35 IN MARCH 1979, 36 IN APRIL 1979, 84 IN MAY 1979, 63 IN MARCH 1980, 86 IN APRIL 1980, AND 204 IN MAY 1980. SAMPLE SIZES FOR BUSHTITS WERE 93 IN MARCH 1979, 87 IN APRIL 1979, 76 IN MAY 1979, 114 IN MARCH 1980, 110 IN APRIL 1980, AND 140 IN MAY 1980

Model I: foraging site

A.  $\ln x_{ijkl} = u + B_i + Y_j + M_k + I_l + BM_{ik} + BI_{il} + MI_{kl} + BY_{ij}$

Chi-square = 43.62, df = 36, P = 0.18

B.  $\ln x_{ijkl} = u + B_i + Y_j + M_k + I_l + BM_{ik} + BI_{il} + MI_{kl} + YM_{jk}$

Chi-square = 48.00, df = 35, P = 0.07

Model II: foraging substrate

$\ln x_{ijkm} = u + B_i + Y_j + M_k + S_m + BY_{ij} + BM_{ik} + BS_{im} + YM_{jk} + MS_{km} + YS_{jm} + BMS_{ikm}$

Chi-square = 27.07, df = 17, P = 0.06

Parameters

- $B_i$  = bird species  $i = 1, 2$
- $Y_j$  = year  $j = 1, 2$
- $M_k$  = month  $k = 1, 2, 3$
- $I_l$  = foraging site  $l = 1, 2, 3, 4, 5$
- $S_m$  = foraging substrate  $m = 1, 2, 3, 4$
- $x_{ijkl}$  = cell frequencies in the  $(x_{ijkl})$  cell
- $x_{ijkm}$  = cell frequencies in the  $(x_{ijkm})$  cell

lower-order interaction terms). To choose the best model from similarly simple models with similarly low P-values, we used four assessment techniques. These were comparisons of: (1) the linear predictors with fitted and observed responses, (2) the nonstandardized residuals with expected responses, (3) the standardized residuals with expected responses, and (4) the standardized residuals with the linear predictors.

Initially we used BMDP4F (Dixon 1983) to determine which level of interaction terms should be included in the final model. These choices ranged from the saturated model (the four-factor interaction and all of those below it) to complete independence of all vari-

ables (the four main effects and no interaction terms). Log-linear models are hierarchical: if a three-way interaction is included in the model, then all two-way interactions between the variables in the three-way interaction are included in the model. Inclusion of interaction terms indicates dependence between the variables in the interaction. For example, a model including the two-way interaction between foraging site and month indicates that foraging sites differed among the 3 months. A model with four main effects (foraging site, month, year, and bird species) and no interaction terms would indicate that foraging site did not differ among months, years, or bird species.

TABLE 2. ESTIMATED PARAMETER VALUES FOR THE SIGNIFICANT INTERACTIONS INVOLVING FORAGING SITE FROM THE TWO LOG-LINEAR MODELS CHOSEN TO DESCRIBE PLANT-SPECIES USE (SEE METHODS)

	Site				
	Gray pine	Live oak	Blue oak	Buckbrush	Other
<b>Model A</b>					
Bird					
Plain Titmouse	0.167	-0.277	0.673	-0.446	-0.116
Bushtit	-0.167	0.277	-0.673	0.446	0.116
Month					
March	-0.392	0.485	-0.535	0.670	-0.229
April	-0.260	-0.048	0.385	-0.064	-0.013
May	0.651	-0.437	0.150	-0.606	0.242
<b>Model B</b>					
Bird					
Plain Titmouse	0.166	-0.279	0.678	-0.449	-0.116
Bushtit	-0.166	0.279	-0.678	0.449	0.116
Month					
March	-0.391	0.487	-0.543	0.672	-0.226
April	-0.252	-0.058	0.400	-0.077	-0.013
May	0.643	-0.429	0.143	-0.595	0.239

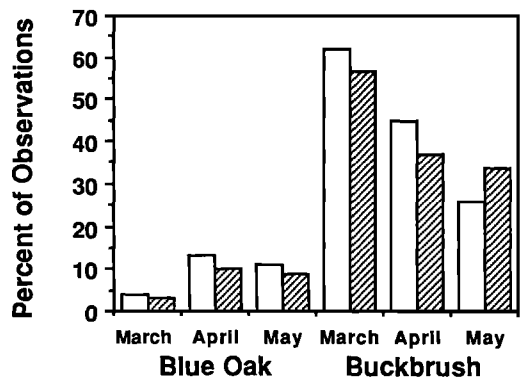
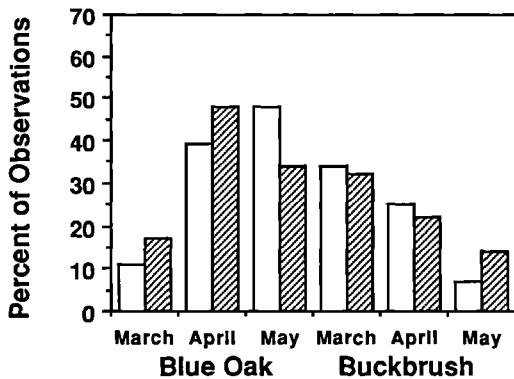
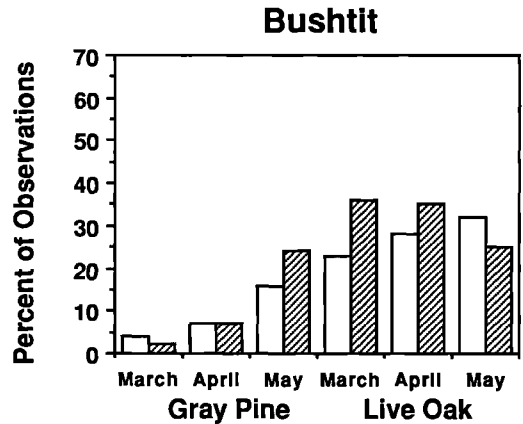
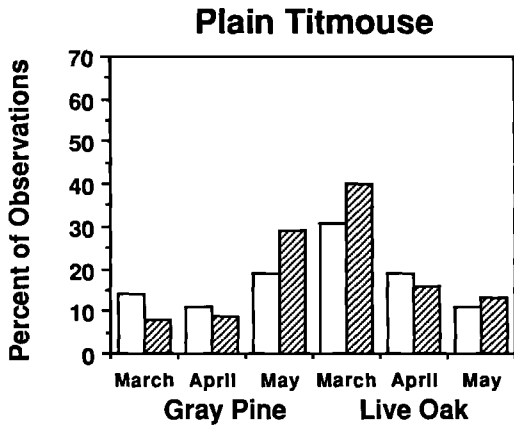


FIGURE 1. Percent of all foraging maneuvers by Plain Titmice on each of the four major plant species in each month in 1979 (open bars) and 1980 (shaded bars). March = phenological intervals 1 and 2, April = phenological intervals 3 and 4, May = phenological intervals 5 and 6. Sample sizes were 35 in March 1979, 36 in April 1979, 84 in May 1979, 63 in March 1980, 86 in April 1980, and 204 in May 1980.

FIGURE 2. Percent of all foraging maneuvers by Bushtits on each of the four major plant species in each month (see Fig. 1 for definition of phenological intervals) in 1979 (open bars) and 1980 (shaded bars). Sample sizes were 93 in March 1979, 87 in April 1979, 76 in May 1979, 114 in March 1980, 110 in April 1980, and 140 in May 1980.

Backward and forward selection procedures from BMDP were examined to select several models that were similarly good, based on their P-values for the log-likelihood test statistic that approximates the chi-square statistic for larger sample sizes. We sought the simplest model that would adequately explain our data ( $P > 0.05$ ). Use of the General Linear Interactive Model, GLIM (Royal Statistical Society 1986), further refined our choice. We could add or delete terms easily and quickly on GLIM and compare linear predictors, fitted, observed and expected responses, and nonstandardized and standardized residuals. The procedures led to two similarly simple models for foraging site and one model for foraging substrate. We next employed the four assessment techniques to choose between the two competing models for foraging site. Based on the

assessment techniques, neither model for foraging site seemed better. Therefore, we present results from both models. Judgments were made on complete models. All terms in the chosen models are significant and their biological meanings are discussed.

For the chosen log-linear model, parameters were estimated to assess the sign and magnitude of each component of each variable in each interaction term. Bishop et al. (1975:62) refer to estimates of parameter values as *u*-terms. The estimates sum to zero across categories. The magnitude reflects the importance of the component, and the sign indicates the direction of the effect. Bishop et al. (1975) give a mathematical description of log-linear models and parameter estimates. A good biological example of the use of parameter estimates is in Page et al. (1985); Schoener (1970),

TABLE 3. ESTIMATED PARAMETER VALUES FOR THE SIGNIFICANT INTERACTIONS INVOLVING FORAGING SUBSTRATE FROM THE LOG-LINEAR MODEL CHOSEN TO DESCRIBE SUBSTRATE USE (SEE METHODS)

Year	Substrate			
	Bark	Foliage	Reproductive parts	Other
1979	0.042	-0.000	-0.169	0.127
1980	-0.042	0.000	0.169	-0.127

Substrate	Month	Bird species	
		Plain Titmouse	Bushtit
Bark	March	0.065	-0.065
	April	-0.007	0.007
	May	-0.058	0.058
Foliage	March	-0.043	0.043
	April	0.251	-0.251
	May	-0.208	0.208
Reproductive parts	March	-0.240	0.240
	April	-0.050	0.050
	May	0.290	-0.290
Other	March	0.218	-0.218
	April	-0.194	0.194
	May	-0.024	0.024

Jenkins (1975), and Harris (1984) provide other biological examples using log-linear models.

## RESULTS

### MODEL I: FORAGING SITE

Based on P-values, simplicity, and the four assessment techniques, GLIM showed that four of the two-way interactions alone created two different but equally satisfactory models (Table 1).

*Within-season changes.* The two species foraged differently among the five sites in the 3 months, as indicated by the significant interactions between months and sites in both models (Table 1). These changes were parallel in the two species. In general, the greater use of live oak and buckbrush and the concomitant lesser use of blue oak by both species in March, the increased use of blue oak in April, and the increased use of gray pine and other sites in May were indicated by the size and sign of the estimated parameter values for the site-by-month interactions (Table 2 and Figs. 1 and 2).

*Yearly differences.* The relative number of observations among plant species was the same in both years (both models excluded the year-by-site interaction).

*Foraging differences between Plain Titmice and Bushtits.* Although parallel changes in site use occurred in the two species, the overall use of plant species was significantly different between the two species, as reflected by the inclusion of

the bird-by-site interaction in both models (Table 1). Overall, Plain Titmice foraged more often on blue oak and Bushtits foraged more often on buckbrush (Table 2 and Figs. 1 and 2).

### MODEL II: FORAGING SUBSTRATE

According to the criteria described above, one simple, satisfactory model was the best for foraging substrate (Table 1).

*Within-season differences and foraging differences between Plain Titmice and Bushtits.* The two species foraged from the four substrates differently across the 3 months, as evidenced by the inclusion of the bird-by-month-by-substrate interaction in the chosen model (Table 1). Plain Titmice emphasized other substrates in March, foliage in April, and reproductive parts in May, while Bushtits foraged from reproductive parts in March, from other substrates in April, and from foliage in May (Table 3).

*Yearly differences.* The use of foraging substrates by the two species differed significantly between years, as indicated by the inclusion of the year-by-substrate interaction in the chosen model (Table 1). However, the relatively small sizes of the estimated parameter values suggested that the weight of this interaction in this model was small (Table 3).

### DIFFERENCES IN FORAGING SITES, SUBSTRATES, AND PLANT PHENOLOGY

Several monthly differences in emphasis of foraging substrates on certain foraging sites par-

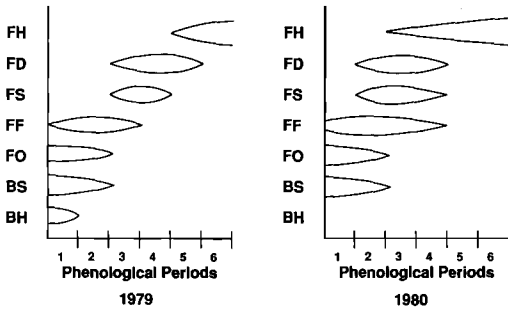


FIGURE 3. Reproductive phenologies of buckbrush in 1979 and 1980. BH = flower buds hard, BS = flower buds swollen, FO = flowers open, FF = full flowers present, FS = fruits set, FD = fruits developing, FH = fruits hard. Dates for phenological periods as follows: 1 = 12 to 23 March 1979, and 10 to 21 March 1980; 2 = 26 March to 6 April 1979, and 24 March to 4 April 1980; 3 = 9 to 20 April 1979, and 7 to 18 April 1980; 4 = 23 April to 4 May 1979, and 21 April to 2 May 1980; 5 = 7 to 18 May 1979, and 5 to 16 May 1980; 6 = 21 May to 1 June 1979 and 19 to 30 May 1980. Widths of symbols are based on relative percentages of total branches in each phenological state. Curves were drawn by hand to connect the points from each 2-week sample.

alleled changes in plant phenology. For example, the peak period of flowering by buckbrush occurred in March and April in both years (Fig. 3), and fruit replaced flowers by the end of April each year. Blue oaks began leafing out in March, and stem elongation and the surge of new leaves occurred by mid-April in both years (Fig. 4). Concomitantly, Bushtits so emphasized buckbrush flowers as a substrate in March of both years that they comprised nearly 50% of all substrates on all foraging sites (Table 4). On buckbrush alone, flowers comprised 71% of the substrates in 1979 and 84% in 1980. Plain Titmice exhibited a similar pattern in March of both years (Table 4), although buckbrush leaves comprised a larger proportion of their foraging substrates than flowers in 1979. Use of buckbrush flowers by both species dropped markedly in April and did not occur at all in May, but both species increased their use of blue oak leaves as a foraging substrate in April and May of both years (Table 5).

## DISCUSSION

Our results of significant within-season differences are like those of many other investigators (Holmes 1966, Busby and Sealy 1979, Alatalo 1980, Rotenberry 1980a). Our yearly differences were not pronounced and did not seem as great as those found by Holmes (1966), Root (1967),

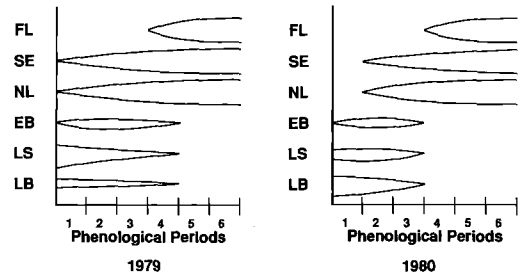


FIGURE 4. Vegetative phenologies of blue oak in 1979 and 1980. LB = leaf buds present, LS = leaf buds swollen, EB = elongated buds, NL = new leaves, SE = stem elongation, FL = full-sized leaves. Dates for phenological periods as in Figure 3. Widths of symbols are based on relative percentages of total branches in each phenological state. Curves were drawn by hand to connect the points from each 2-week sample.

Busby and Sealy (1979), Rotenberry (1980a), Wagner (1981b), and Szaro et al. (this volume).

Several researchers have found that within-season trends in the foraging behavior and diet of one species often parallel those of other species in the same habitat (Morse 1970, Alatalo 1980, Rotenberry 1980a, this study), probably because prey availability changed (e.g., Holmes and Pitelka 1968). Seasonal changes in the foraging behavior of gnatcatchers, and the availability of their prey in a California oak woodland, corresponded with plant phenology (Root 1967). We believe that within-season shifts in the foraging behavior of the Plain Titmice and Bushtits in this study also resulted from changing prey availability in relation to different stages of plant phenology.

Observer differences cannot be ruled out as contributing to some of the yearly differences observed in this study, although we do not believe they had a major effect. For example, the patterns of shifting foraging substrates on certain sites with plant phenology were similar in both years, even though only one observer sampled in 1979 but three observers sampled in 1980. Our ability to detect yearly differences may have been increased by the disparity in sample sizes between years. However, each of our monthly sample periods included more than 30 observations of each species, thus exceeding the minimum sample size recommended by Morrison (1984a) for studies of avian foraging behavior (but see Brennan and Morrison, this volume), and the bird-by-month and bird-by-year interactions in the models for foraging sites and substrates act as blocking factors for sample size differences (M. F. Bryan, pers. comm.).

TABLE 4. PERCENT OF FORAGING ON EACH SUBSTRATE ON BUCKBRUSH (IN RELATION TO FORAGING ON ALL SITES AND SUBSTRATES) BY PLAIN TITMICE AND BUSHTITS DURING THE SPRINGS OF 1979 AND 1980

Substrate	1979			1980		
	March	April	May	March	April	May
Plain Titmouse						
Branch	0	3	1	2	4	3
Flower	11	6	0	22	2	0
Flower bud	0	0	0	2	0	0
Fruit	0	0	0	0	0	1
Leaf	17	11	6	3	13	8
Twig	6	6	0	3	4	3
Bushtit						
Branch	1	2	3	1	1	3
Flower	44	9	0	48	4	0
Flower bud	0	0	0	0	0	0
Fruit	0	0	0	0	9	0
Leaf	13	23	16	6	19	26
Twig	4	10	8	2	4	5

Our results caution against generalizations made from data gathered during one month, one year, or for differing numbers of months and years. Ignoring either short- or long-term variations in foraging behavior can lead to oversimplifications and even obscure ecologically significant patterns. We also think this can happen when researchers uncouple components of foraging behavior for ease of analysis. For example, important interactions between foraging substrates and foraging sites were missed in this study when we created models for foraging sites independent from foraging substrates. The birds

shifted their emphasis on substrates from buckbrush flowers to blue oak leaves in a similar pattern in both years. Because of our relatively small sample sizes, important relationships between these site-substrate combinations could be shown only in tables and figures. We suggest that researchers with larger data sets include foraging site and substrate in the same multiway contingency table for analysis. Structural zeros (cells in the contingency table that necessarily contain zeros; for example, the cell for buckbrush flowers in May contained a zero because buckbrush does not flower in May) will inevitably occur with

TABLE 5. PERCENT OF FORAGING ON EACH SUBSTRATE ON BLUE OAK (IN RELATION TO FORAGING ON ALL SITES AND SUBSTRATES) BY PLAIN TITMICE AND BUSHTITS DURING THE SPRINGS OF 1979 AND 1980

Substrate	1979			1980		
	March	April	May	March	April	May
Plain Titmouse						
Branch	8	5	17	5	1	9
Catkin	0	0	0	0	1	0
Large branch	0	5	0	3	0	<1
Leaf	0	25	25	5	38	20
Leaf bud	3	0	0	3	0	0
Trunk	0	0	1	0	0	<1
Twig	0	3	5	2	7	4
Bushtit						
Branch	0	0	1	0	1	2
Catkin	0	1	0	0	2	0
Large branch	1	1	0	1	0	0
Leaf	0	10	8	0	6	4
Leaf bud	1	0	0	1	0	0
Trunk	0	0	0	1	0	0
Twig	2	1	1	0	1	3

changes in plant phenology. However, the BMDP program can be instructed to deal with them and to adjust the degrees of freedom appropriately. Sampling zeros are problematic only when the marginals (row or column totals) are zeros. A large proportion of the literature on avian foraging behavior includes data pooled across months and years and data analyzed separately for foraging site and substrate, but the extent to which such procedures may have biased conclusions is unknown.

#### ACKNOWLEDGMENTS

K. L. Purcell and L. V. Ritter collected field observations and shared ideas on avian foraging behavior

and plant phenology. R. M. Caldwell helped collect phenological data, keypunch data, and offered support and advice throughout the study. D. A. Duncan, J. R. Larson, D. L. Neal, and R. D. Ratliff helped formulate appropriate phenological methods. G. W. Salt provided support, advice, and criticism throughout the study. J. A. Baldwin, M. F. Bryan, S. R. Mori, G. W. Bell, and W. R. Rice offered statistical help. C. J. Evans, J. H. Harris, S. A. Laymon, B. A. Maurer, G. W. Page, and L. E. Stenzel helped clarify the use of log-linear models for us. R. L. Hutto, B. A. Maurer, K. L. Purcell, C. J. Ralph, and M. G. Raphael reviewed an earlier version of the manuscript. We appreciate the help of all.