# Covariance Patterns Among Birds and Vegetation in a California Oak Woodland[1]

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**Abstract:** We sampled characteristics of vegetation and estimated abundances of bird species on 23 plots representing a continuum of tree densities of the blue oak phase of the Coast Range foothill woodland near Hopland, California. Fifty-one bird species were found breeding. Cavity-nesters dominated the bird community in number of species and individuals. Cavity-nesters used a variety of tree species for nesting, highlighting the importance of tree species richness. Large deciduous oaks were found to be important as granary trees for acorn woodpeckers, as well as substrates for nest cavity excavation by primary cavity nesters. Large evergreen trees were important in providing natural cavities to many secondary cavity nesting bird species. Both individual bird species and guilds showed few covariations with tree density. We discuss why a guild approach is not always a useful way to describe relationships between bird abundance and vegetation. Effects of spatial scale and plot size on observed bird/habitat relationships are discussed.

Approximately eight million hectares in California, or 20 percent of the state's land area, are vegetated by one or more species of oak (*Quercus* spp.). The rate of harvest of oak trees in California, however, has increased to the point where many oak habitats are threatened. Fuelwood harvest, for example, has increased steadily since 1959, turning sharply upward in 1973 (Menke and Fry 1980, Walt and others 1985). The rate of conversion of oak woodlands to pasture land and for agricultural, residential and commercial development has also increased markedly since 1973 (Bolsinger 1987). Unfortunately, the harvest of oaks may severely reduce habitat quality for many wild animals, or preclude some wildlife species entirely. A further problem is that many oak woodlands are experiencing very poor regeneration and extremely low seedling and sapling survival. The exact cause for the low recruitment is unknown, but has been attributed in some cases to excessive predation by small mammals (Griffin 1980, Knudsen 1987) and overgrazing by deer and cattle (Bowyer and Bleich 1980, Griggs 1987).

In the face of these threats and an increasing trend of exploitation, it is particularly disturbing to discover that there remain significant gaps in our understanding of the relationship between California wildlife and oak woodlands. Muick and Bartolome's (1985) listing of studies conducted in California oak habitats between 1953 and 1985 included l6 bird studies, 15 mammal studies, and only one reptile and amphibian study. Few of these studies addressed the results of habitat disturbance or habitat loss on the wildlife community.

California oak woodlands are particularly rich in bird species—approximately 110 species of birds can be observed during the breeding season (Verner 1980). Verner (1983) reported that oak woodlands in North America rank among the top three habitat types in the number of bird species for which they provide breeding habitat. In order for a resource manager or agency to make recommendations on the management of oak woodlands for birds, more information is needed on how birds respond to variation in the vegetation structure and composition of these habitats. For example, at this time the density, size, or spatial distribution of trees required to meet the needs of the bird community on managed woodlands is unknown. It is important that the needs of the wildlife community be considered along with economic and aesthetic considerations in the management of California's oak woodlands.

Two silvicultural options which can easily be targeted for management are the residual density of trees remaining after the harvest and tree species composition. Tree density and tree species composition can be optimized for a variety of purposes including regeneration potential, forage production, aesthetic quality, and wildlife value. This paper reports on the relationship among various attributes of the breeding bird community and the vegetative community, primarily tree density and tree species composition. The relationship of the bird community to the vegetative community is defined by changes in bird species composition and changes in the abundance of particular bird species. In addition, we described the nest site selection patterns of the cavity nesting birds and granary tree selection by acorn woodpeckers. Selection was explored in terms of used and available tree species and tree diameters.

## STUDY AREA

The study area was located at the University of California Hopland Field Station five miles east of Hopland, in Mendocino County, California. The dominant vegetation was the blue oak (*Quercus douglasii*) phase of the Coast Range foothill woodland (Griffin 1977). Blue oak was the dominant tree species in association with valley oak (*Q. lobata*), interior live oak (*Q. wislizenii*), California black oak (*Q. kelloggii*), Oregon white oak (*Q. garryana*), California bay (*Umbellularia californica*), and buckeye (*Aesculus californica*). Annual grasses and forbs dominated the ground cover. Adjacent vegetation types in-

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cluded chaparral, mixed hardwood and conifer forest, and meadows. Sheep grazing was the primary land use.

The topography was characterized by moderate to steeply sloped hills. The study area had a westerly aspect and covered an elevational gradient ranging from 200 to 1000 meters. The steep westerly aspect promoted vegetative growth along east-west strips aligned with intermittent streams and ravines. The ravines, dominated by live oaks, bay, and shrubs, dissected upland habitats, dominated by deciduous oaks. Average rainfall was 90 cm, generally occurring between September and June.

## METHODS

### Study Plots

Twenty-three, five ha (100 by 500 m) study plots were established throughout the continuum of available tree densities in the 2,143 ha study area. Plots were systematically selected to represent a steep gradient in tree density. For individual plots, uniform tree density and distribution within and adjacent (within 50 m of plot boundary) to the plots were criteria for placement. Plot width was based on the ability to detect and accurately map the location of birds. Plots were spaced at least 100 m apart and dispersed throughout the study area.

### Censusing

The fixed-width belt transect method was used to collect data on the bird community (Christman 1984). Each plot was censused once per week between late March and mid-June during 1986 and 198'7 for a total of ten censuses per plot per year. Censuses were conducted between 0500 and 0900 Pacific Standard Time. A census consisted of walking down the center transect line of a plot at a pace of 50 m every six minutes and mapping the location and recording the behavior of all birds detected within 50 m on either side of the transect line. The total area censused for each plot was 5 ha. Each census required one hour to complete. Bird species abundances were described by estimating the mean number of detections occurring within 50 m of the transect line per census for each bird species on each plot (1986 and 1987 data combined).

### Nest Search

During the spring of 1986, we located as many nests as possible of all breeding species. During 1987, we focused on locating nests of cavity nesting species. Nests were located opportunistically and by active search.

### Vegetation Measurements

The vegetation on each plot was described by mapping the location and recording descriptive information on each individual woody plant. We recorded the following information for each plot: species, total height, diameter at breast height (DBH), number of natural and excavated cavities, and use as a granary tree. Tree height was measured primarily by ocular estimation. DBH was measured with a diameter tape. Trees with natural and/or excavated cavities were each categorized as containing 0, 1-3, or >3 cavities. Cavities were counted when the entrance appeared of suitable dimensions for use by cavity nesting birds. Acorn woodpecker granary tree use was categorized as: no evidence of use, < 10 percent use, or > 10 percent use. These categories reflect the variation in use patterns observed on our study plots.

### Data Analysis

A variety of univariate and multivariate analyses were used on each data set. Normality of the data was assessed by visual inspection of histograms. Some variables required normalizing transformations. Analysis of variance and Tukey's test were used to describe relationships between tree diameter and cavity abundance, and between tree diameter and use as granary trees. Chi-square goodness-of-fit tests were used to test for differences in use versus availability of tree species for cavities and granary trees. Bonferoni's normal statistic (Neu and others 1974) was used to determine which tree species were used greater or less than available. A total of 412 trees, with $\geq 1$ excavated cavity, were assumed available for secondary cavity nesters, and we assumed that all trees ($n = 16{,}066$) on our plots were available for primary cavity nesters. An alpha of $\leq 0.05$ was used for all tests of significance.

We estimated the value of a large number of structural and compositional vegetation variables. The major axes of variation in the vegetation among plots were estimated by principal components analysis (PCA) from a correlation matrix of 22 untransformed vegetation variables described by their mean values and counts for each study plot. Variables used in the analysis represented both the vegetation structure and composition of each study plot. The PCA included a varimax rotation of the principal components followed by ordination of each study plot according to its standardized factor scores.

Weighted average positions of the 10 most common bird species were computed for the three-dimensional vegetation space estimated by PCA. Species coordinates were computed by weighting each plot's ordination, scores by the species' abundance on that plot, summing these weighed scores and then dividing by the sum of the weights.

We investigated the potential influence of plot size on observed vegetation patterns. Canopy closure, which was highly correlated with tree density and distribution, was used as an indicator of the vegetation heterogeneity in the study area. Canopy closure was estimated at four different plot sizes (5, 10, 20, and 50 ha). Concentric 10, 20, and 50 ha plot boundaries were drawn on mylar overlays around the boundary of the 5 ha study plot. Canopy closure was estimated with a dot grid by overlaying the mylar on air photographs (1:7000 scale) of each study plot and counting dots obscured by overstory canopy.

All possible subsets regression was used to select a "best" subset of vegetation variables (independent variables) to explain variation in the abundance of individual bird species and bird guilds (dependent variables). Bird species were grouped into eight guilds based on foraging behavior (bark foragers, air salliers, foliage gleaners and ground foragers), nesting behavior (primary cavity nesters and secondary cavity nesters), and season of residence (winter residents and migrants). All possible subsets regression using Mallow's Cp criterion was chosen because it provided a "best" subset which minimizes the total mean squared error of fitted values (Neter and others 1985:421). A set of 11 variables describing the composition and structure of the vegetation was available as independent variables. These included numbers per 5 hectares of the following tree species: blue oaks, black oaks, white oaks, evergreen oaks, buckeyes, shrubs, and snags. Other variables include number of cavities, canopy cover, average basal area, and tree diversity. The abundance of individuals of each species and bird guild were used as dependent variables.

## RESULTS AND DISCUSSION

### *Bird Community*

Seventy-two bird species were detected during censuring in 1986 and 1987. Based on territorial behaviors, 49 were believed to be breeding species. These results provide additional confirmation of the richness of breeding bird species in California oak woodlands (Verner 1980). Relative to other California oak woodlands, the Hopland Field Station had high numbers of breeding bird species. Block (1989) recorded a range of 40-43 breeding bird species detected in three other oak woodlands in California during the same time period. The high number of breeding bird species in our study area may be partially attributed to the relatively high annual rainfall per year, and proximity. to conifer dominated habitats. The latter factor accounts for a number of observed species that were near the southern limit of their breeding distribution.

Of the ten most abundant bird species detected over all study plots, six were cavity nesting species (table 1). Primary and secondary cavity nesters comprised approximately 25 percent (12 species) of the breeding bird species and almost 60 percent. of the breeding individuals (fig. 1). Our estimate of the relative number of cavity nesting species is comparable to conifer. dominated habitats across the western United States (Scott and others 1980, Raphael 1981). However, our estimate of the relative density of cavity nesters is considerably higher than for most temperate breeding bird communities (Scott and others 1980).

**Table 1**—***Ten most abundant breeding bird species across all study plots, Hopland, CA (1986-1987)***

| BIRD SPECIES | #/40 HA[1] | S.E.[2] |
|---|---|---|
| VIOLET-GREEN SWALLOW[3] | 58.2 | 5.0 |
| PLAIN TITMOUSE[3] | 49.0 | 2.6 |
| ACORN WOODPECKER[3] | 25.6 | 2.5 |
| LESSER GOLDFINCH | 20.2 | 2.8 |
| AMERICAN ROBIN | 16.4 | 2.0 |
| WHT-BREASTED NUTHATCH[3] | 13.7 | 1.2 |
| SCRUB JAY | 11.0 | 1.5 |
| MOURNING DOVE | 10.5 | 1.2 |
| EUROPEAN STARLING[3] | 10.3 | 2.5 |
| WESTERN BLUEBIRD[3] | 10.2 | 1.3 |

**[1] Abundance estimates am mean number of detections over all plots. 1986 - 1987.**
**[2] Standard error of the mean abundance.**
**[3] Cavity nesting species.**

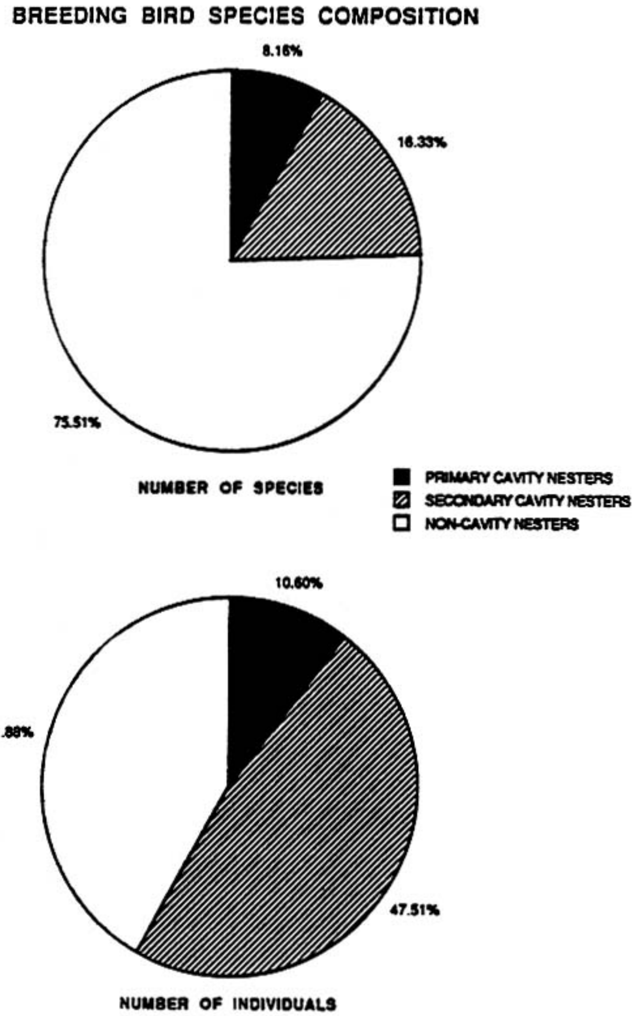


**Figure 1—Proportion of the breeding bird community comprised of cavity nesting (primary and secondary) and open-nesting species. Abundances are estimated from census data for all 23 study plots during both breeding seasons (1986 and 1987).**

## Vegetation

We counted approximately 16,000 trees of eight oak and four other tree species, identified them to species, and characterized their structure (table 2). When ordered by number of trees, the study plots represented a smooth, but steep, gradient in tree density, with densities ranging from 20.2 to 403.6 trees per ha.

The relative abundance of tree species was influenced by elevational variation among plots (fig. 2). For example, blue oak and buckeye were more abundant on lower elevation plots, whereas white oak and bay were more abundant on higher elevation plots. In general, tree species evenness increased with elevation.

Six principal components with eigenvalues > 1.0 described 89 percent of the variation in vegetation structure and composition among plots. Our discussion is limited to the first three principal components which described over 55 percent of the vegetation variation among plots (fig. 3). Principal component 1 (PC 1; 21.1 percent of the explained variation) represented variation in tree density among plots, the primary objective when the plots were systematically selected. PC 2 (20 percent) represented variation in the number and basal area of the most abundant broadleaf evergreen species. One outlier plot ac-

**Table 2—*Tree species detected based on data from all study plots, Hopland, California 1987.***

| COMMON NAME | SCIENTIFIC NAME | FREQ[1] | STEMS[2] | RANGE[3] |
|---|---|---|---|---|
| **OAK TREE SPECIES** | | | | |
| **Blue Oak** | ***Quercus douglasii*** | **100** | **467.1** | **5 - 1643** |
| **Interior live oak** | ***Quercus wislizenii*** | **100** | **63.4** | **12 - 182** |
| **Coast live oak** | ***Quercus agrifolia*** | | | |
| **Canyon live oak** | ***Quercus chrysolepis*** | | | |
| **Valley oak** | ***Quercus lobata*** | **91** | **58.3** | **0 - 423** |
| **Oregon white oak** | ***Quercus garryana*** | | | |
| **Black oak** | ***Quercus kelloggii*** | **78** | **26.9** | **0 - 143** |
| **Oracle oak** | ***Quercus morehus*** | **70** | **2.8** | **0 - 20** |
| **OTHER TREE SPECIES** | | | | |
| **Buckeye** | ***Aesculus californica*** | **83** | **56.9** | **0 - 350** |
| **California bay** | ***Umbellularia californica*** | **70** | **14.0** | **0 - 86** |
| **Madrone** | ***Arbutus menzesii*** | **48** | **5.1** | **0 - 52** |
| **Oregon ash** | ***Fraxinus latifolia*** | **4** | **0.2** | **0 - 5** |

[1] **Percent frequency of occurrence across all plots.**

[2] **Number of stems > 5 cm DBH per 5.0 ha plot.**

[3] **Range in number of sterns per plot.**

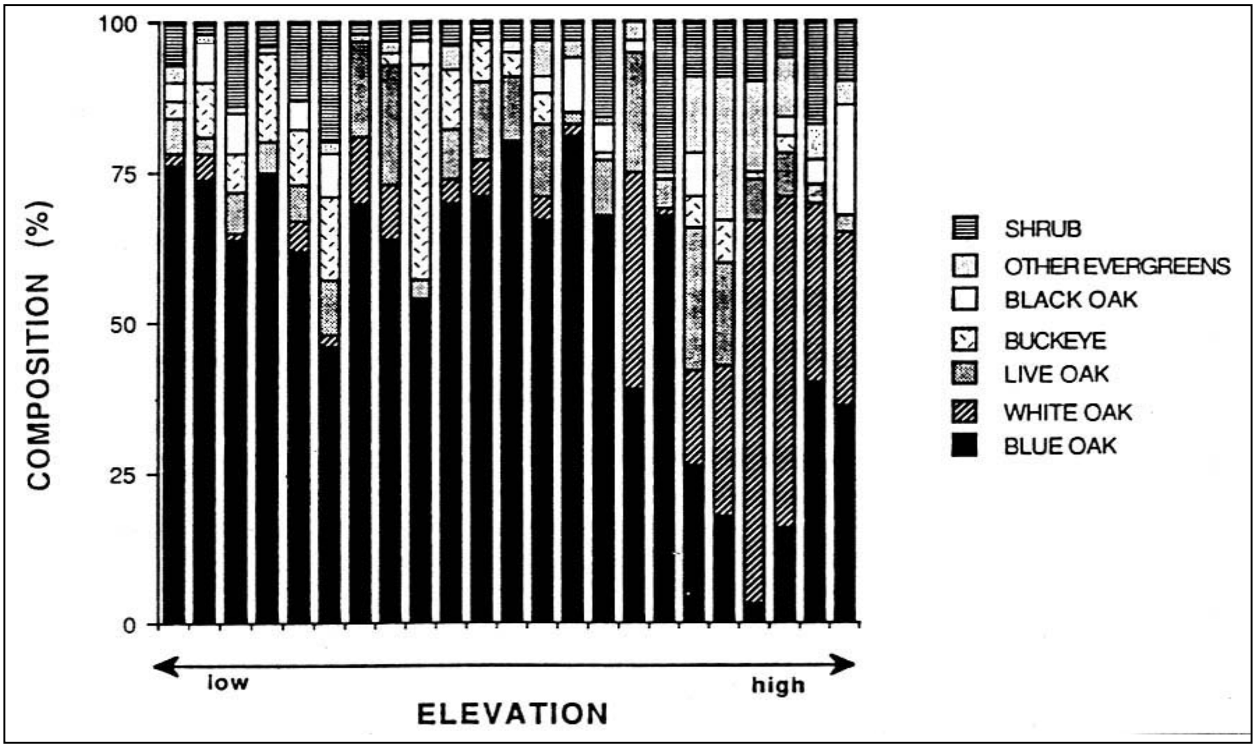


**Figure 2—Tree species composition of each study plot, with the plots arranged according to elevation (range was 200-975m above sea level).**

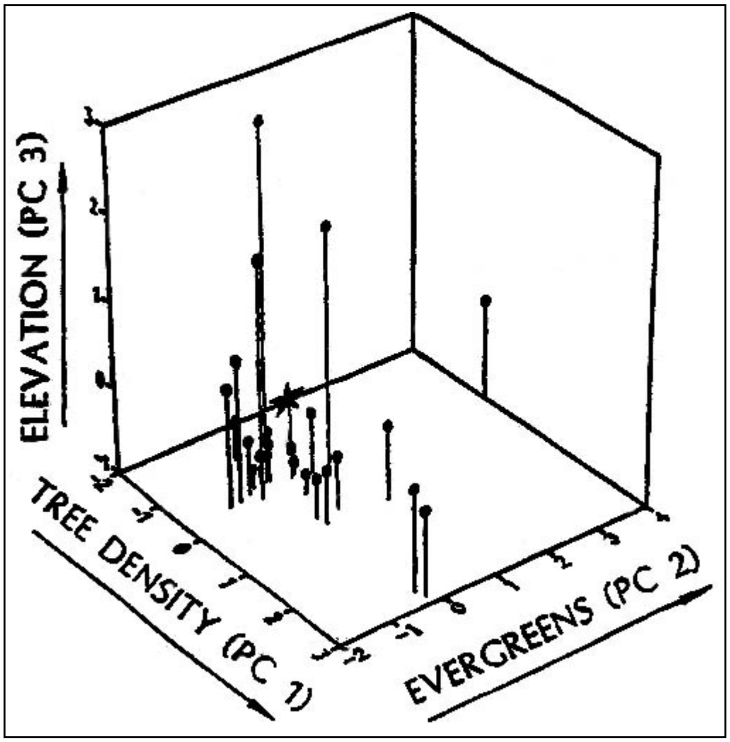


Figure 3—Ordination of the 23 study plots along the first three principal components. Axis 1 represents variation in the number of trees and shrubs, axis 2 the number of live oak and madrone trees per plot, and axis 3 vegetation characteristic that changed with elevation. The star in the figure indicates the approximate, weighed location of the 10 most abundant bird species in this vegetation space.

counted for the majority of the variation explained by this component. Most of the plots did not differ greatly along PC 2. PC 3 (14 percent) represented a gradient from blue oak (at lower elevations) to white oak and bay (at higher elevations), and paralleled an underlying gradient in tree species composition. In general, most vegetation variation among our plots was in tree density, and tree species composition which was influenced by the physical and biological variables associated with changes in elevation.

## Covariation of Bird Abundance and Tree Density

At the scale of 5 ha plots, variation in overall bird abundance and bird species richness was not strongly associated with variation in tree density (n = 23; r = -0.25, p = 0.17 and r = 0.00003, p = 0.43, respectively), even though we had sampled a steep gradient.

When birds were grouped by foraging or nesting guild, the number of species in each group ranged from three to 19. The abundance of individual bird groups was not strongly associated with changes in tree density. The secondary cavity nesting guild showed the strongest relationship with variation in tree density, declining in abundance with increasing tree density (fig. 4a; r = -0.384, p = 0.038). Though significant, the magnitude of the correlation coefficient indicates that little of the abundance variation within this guild was explained by changes in tree density.

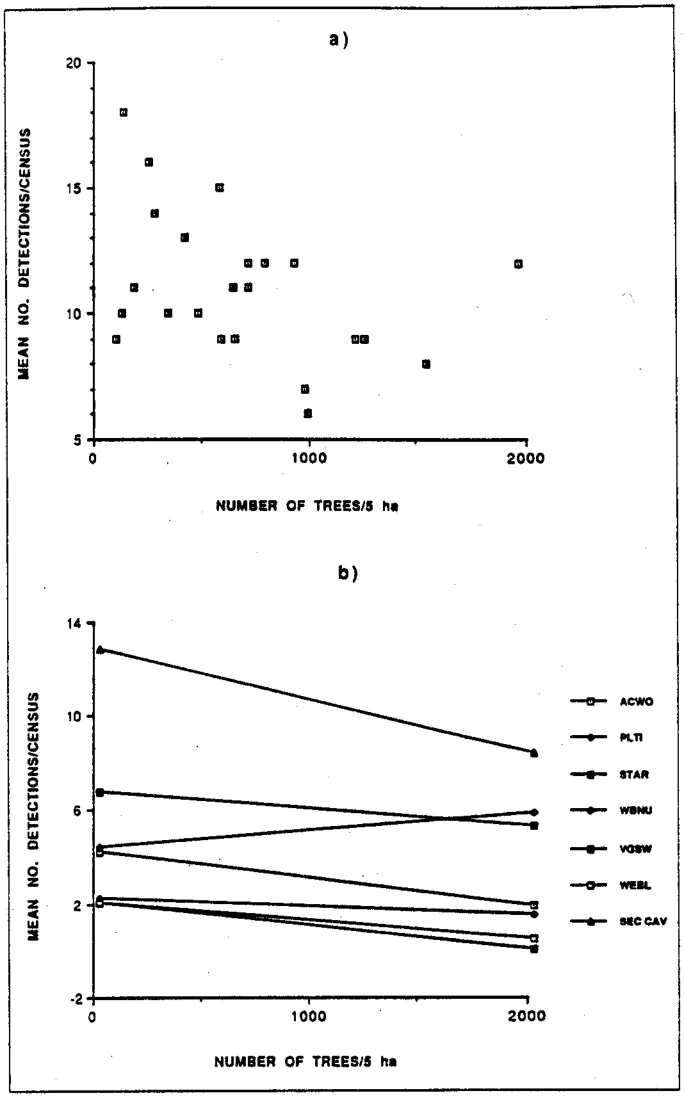


Figure 4—Mean number of detections per census of secondary cavity nesting species as a function of tree density. Estimates are from all 23 study plots: a) bivariate scattergram of the mean number of detections for the entire guild (r = -0.384, p = 0.035). b) regression lines for individual species.

The secondary cavity nesting species illustrate why a guild approach is not always a useful way to describe relationships between bird abundance and vegetation. In our study, not all species in this guild showed a consistent response to variation in tree density (fig. 4b). The abundance of all species, except plain titmouse, decreased with increasing tree density. The individual regression lines (fig. 4b) illustrate that different species within a group do not always show the same pattern of response to vegetation variation, even when the characteristic may affect the abundance or availability of a key resource (i.e., availability of cavities for secondary cavity nesters). Variation in habitat relationships among members of a guild may reflect variation in other life history characteristics. Secondary cavity nesters in our study varied in the food resources they exploited (omnivorous versus insectivorous), foraging strategies (salliers, gleaners, and hawkers), and foraging substrates (ground, leaf, bark, and air).

Habitat relationships of the ten most abundant bird species and Nuttall's woodpecker (the second most abundant primary cavity nester) were of special interest because they comprised almost 60 percent of all the individuals in the bird community. Based on the independent variables selected in regression analyses and other variables with which they were highly correlated, a number of species showed similar habitat associations (table 3). Five of the seven cavity nesters and one open nester were more abundant on plots with large diameter (>50 cm DBH) trees and an abundance of cavities, indicating an association with low tree densities (<100 per ha). The remaining two cavity nesters and one open nester were more abundant on plots with moderate tree densities (100 to 180 per ha). Two open nesters were more abundant on plots with moderate tree densities, but on plots. where the distribution was clumped because of dense vegetation in ravines. Ravines were typically occupied by dense patches of evergreen trees which provided cover and nesting substrates in otherwise open plots.

No abundant bird species showed a strong association with high tree density (>180 per ha). Areas with high tree densities, however, appeared to provide habitat for some less abundant species, specifically pygmy owl, brown creeper, barn owl, and turkey. The abundances of these species covaried positively with tree density, but detections were too few for statistical significance. Areas with high tree density may be associated with lower levels of disturbance from grazing animals; dense plots were not grazed as heavily because of reduced forage. Dense plots may have offered greater cover from avian predators, and provided concealed roost sites.

An additional way to explore a species' response to multivariate habitat gradients is in the context of the vegetation PCA. We plotted the location of the 10 most abundant species (table 1) in the three-dimensional PCA space (fig. 3). Because all points, except the European starling, fell very near the origin (0,0,0), we have simply indicated this position by a star (fig. 4). A common location for all these points indicates that the most common species did not vary systematically with either tree density or elevation. This pattern arose despite the fact that most species showed substantial density variation across plots (coefficients of variation > 40 percent). The weighted locations near the origin indicate that none of the abundant species found optimal conditions at the extremes of any vegetation gradient.

The lack of strong covariation between tree density and bird species abundance may be partially attributed to the strong association of tree density with other vegetative characteristics including average tree diameter and tree species composition. For example, plots with the highest tree density were stands of small diameter blue oak, and open plots were invariably dominated by large diameter blue and white oaks. In addition, our estimate of tree density contained no information about the distributional pattern of trees within a plot. Unfortunately, the levels of resolution at which bird species perceive their environment (grain) is unknown to us. The distribution of trees (evenly spaced versus clumped) at some unknown spatial scale may have more influence on habitat quality than the overall tree density based on our 5 ha study plots.

## Resource Use by Cavity Nesting Birds

### Tree Species Use

We assume the distribution and abundance of natural and excavated cavities to be important to cavity nesting birds. Comparisons were made between the number of trees of a given species across all plots and the relative number of trees of each species with one or more cavities (fig. 5). Of the more than 16,000 trees measured on our plots, 412 (2.5 percent) had at least one excavated cavity, and 2,207 (13.7 percent) had at least one natural cavity. The number of cavities varied by tree species (fig. 5). The majority of natural and excavated cavities occurred in blue oaks, though less than expected based on the abundance of this species. Natural cavities occurred significantly more frequently in evergreen tree species (primarily live oak) than expected. A greater than expected number of evergreen and buckeye trees had natural cavities compared to their availability (fig. 5b). White oaks contained a significantly greater number of excavated cavities than expected based on their availability (fig. 5a). White oaks made up nine percent of the trees measured, yet comprised 30 and 36 percent of the trees containing 1-3 and

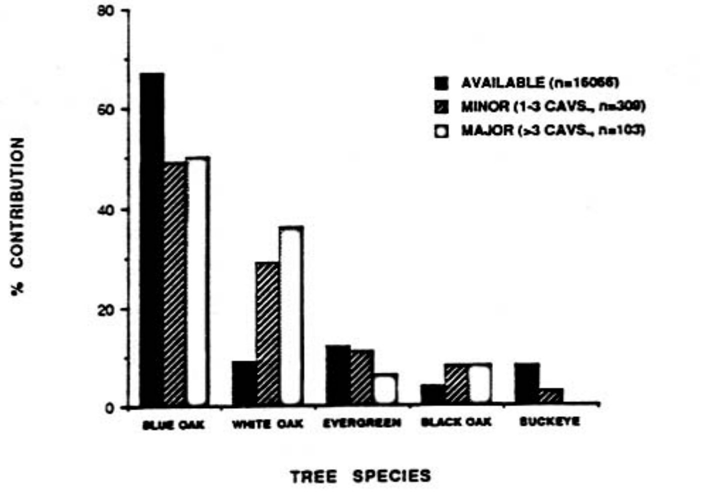
**Table 3**—*General habitat associations of 11 common bird species, Hopland, California 1987-1988.*

| LOW TREE DENSITY,[1] LARGE TREE DIAMETER | MODERATE TREE DENSITY, MODERATE[2] TREE DIAMETER | MODERATE TREE DENSITY, MODERATE TREE DIAMETER, BUT CLUMPED DISTRIBUTION |
|---|---|---|
| CAVITY NESTERS | | |
| Acorn woodpecker | Plain titmouse | |
| Nuttall's woodpecker | Violet-green swallow | |
| White-breasted nuthatch | | |
| Western bluebird | | |
| European Starling | | |
| OPEN NESTERS | | |
| Mourning dove | Lesser Goldfinch | Scrub Jay |
| | | American robin |

[1] Less than 100 trees per ha; average DBH of 45 cm.

[2] 100-180 trees per ha; average DBH of 31 cm.

a) Excavated



b) Natural

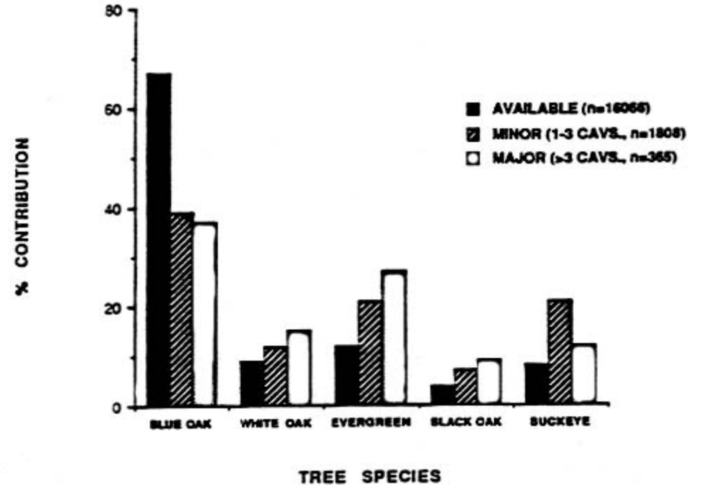


**Figure 5—Excavated (a) and natural (b) cavity use by tree species for cavity nesting birds compared with tree species availability.**

>3 excavated cavities, respectively. Black oaks comprised a small proportion (<5 percent) of the total number of trees; however, they also contained significantly more excavated cavities than expected.

## Natural versus Excavated Cavity Use

Both natural and excavated cavities were important to cavity nesting species in the study area. Based on 306 nests from seven species of cavity nesting birds, we compared their relative use of excavated and natural cavities as nest sites (fig. 6). Species were arranged from those exclusively using excavated cavities (acorn and Nuttall's woodpeckers) to predominantly natural cavity nesters (plain titmouse and white-breasted nuthatch). All secondary cavity nesters used excavated cavities to some degree; however, the majority (65 percent) of nests occurred in natural cavities. The extent to which natural cavities were used for nesting by secondary cavity nesters was high compared to oak woodlands at the San Joaquin Experimental Range (34 percent use; J. Waters, pers. comm).

In addition to the differential use of cavity types, cavity nesters chose to nest in a number of different tree species (fig. 7). Acorn woodpeckers excavated cavities most often in blue oaks and chose white oaks in proportion to their availability (fig. 7b). We did not find any Nuttall's woodpecker nests in white oaks even though more excavated cavities occurred in white oaks than expected. Nuttall's woodpecker nested primarily in blue oaks, evergreens, and black oaks. The number of plain titmouse nests in excavated cavities did not differ from expected for any tree species (fig. 7a). White-breasted nuthatches also chose tree species with natural cavities in proportion to availability (fig. 7c). These two species are potential competitors for cavities since they both preferred natural cavities, chose similar tree species, and both were early nesters (late March). The introduced European starling used excavated cavities exclusively, with blue oak and white oak tree species chosen in equal numbers. Western bluebirds chose 67 percent excavated and 33 percent natural cavities, with blue oak being the dominant choice (>60 percent in both cases).

Even though a large number (488) of buckeye trees contained natural cavities, it was not selected as a nest tree. We speculate that cavities in buckeye were too low to the ground and therefore easily accessible by snakes. Gopher snakes were seen in cavities on at least six occasions, and destroyed at least three occupied nests.

## Tree Diameter

The abundance of both natural and excavated cavities covaried positively with tree diameter for most tree species. The number of natural cavities increased significantly with diameter when all tree species were combined (fig. 8a; F = 632, df = 2, $p < 0.001$). The number of excavated cavities also increased significantly with tree diameter for all species combined (F = 384, df = 3, $p < 0.001$, fig. 8b) and each individual tree species except evergreen oaks and buckeye. These associations occur for two primary reasons: 1) larger trees are generally older and have had greater time to accumulate cavities; and 2) older trees are more likely to have experienced loss of limbs and disease, factors which promote natural and excavated cavities.

Collectively, the results of tree species and diameter use patterns suggest that large (> 50 cm DBH), old trees of both

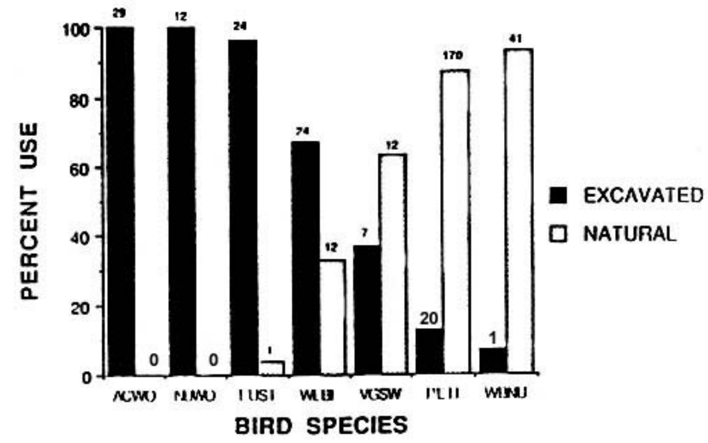


**Figure 6—Proportions of cavity type used (excavated or natural) for nesting by seven species of birds, 1987 and 1988.**

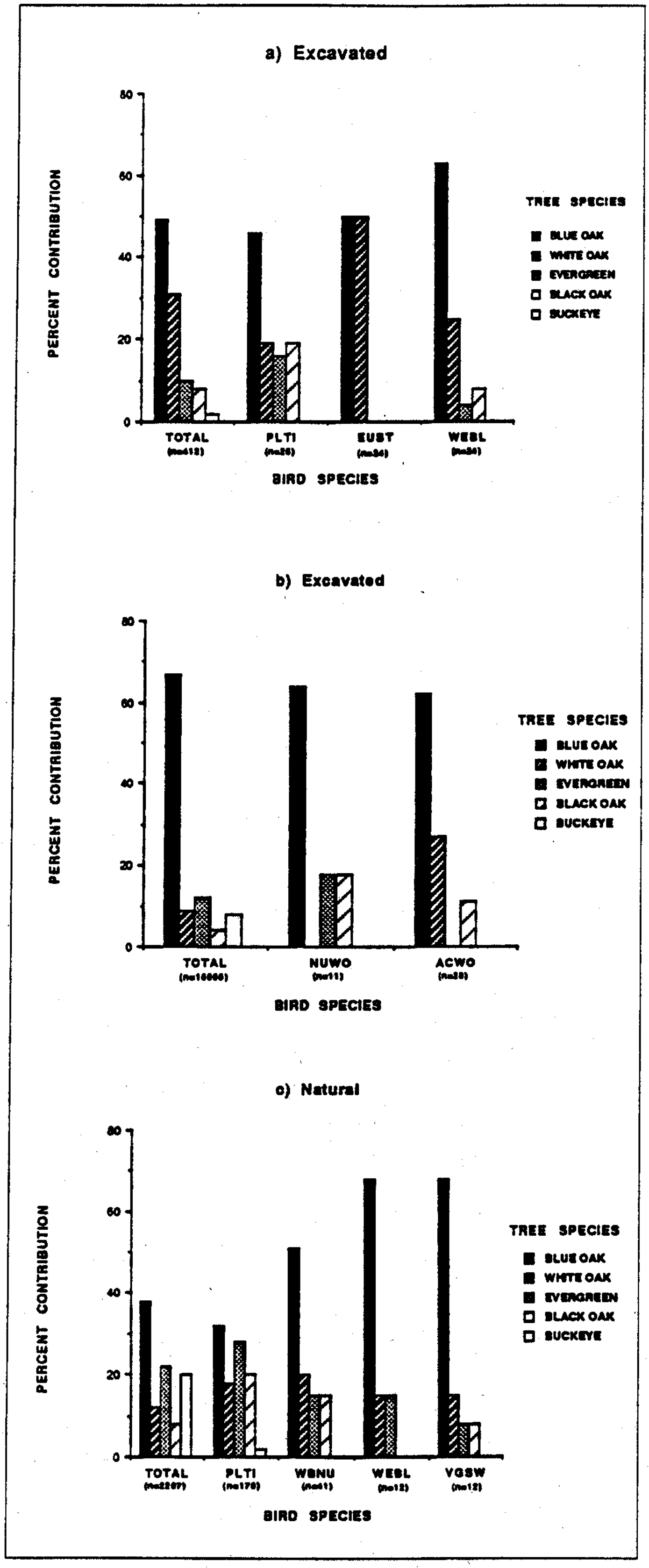


Figure 7—Nest tree selection by: a) secondary cavity nesters, and b) primary cavity nesters using excavated cavities, and c) secondary cavity nesters using natural cavities.

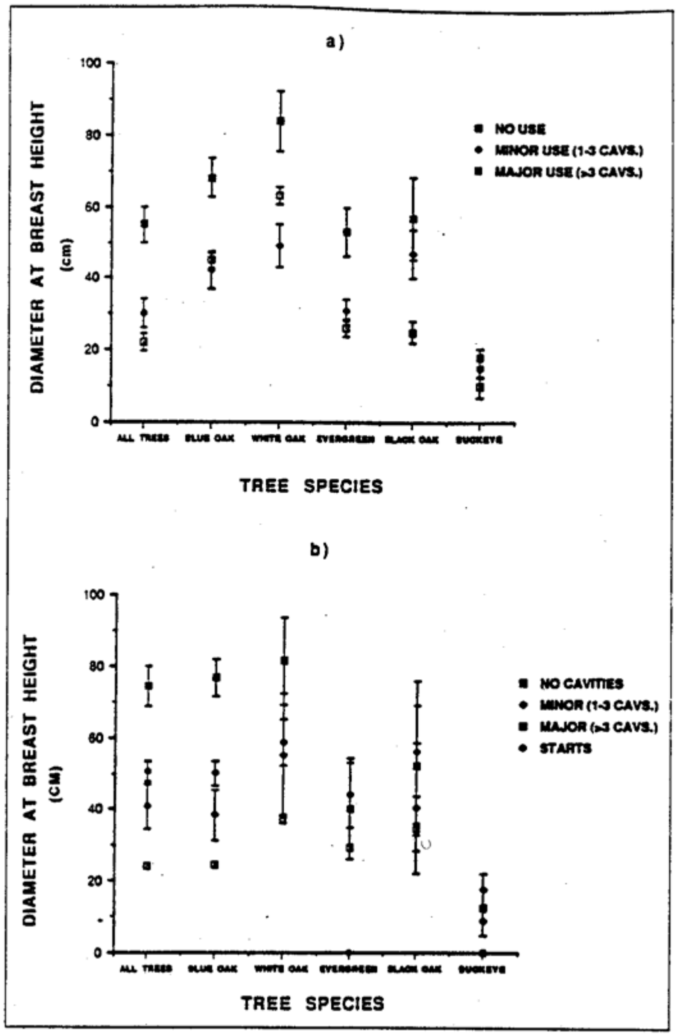


Figure 8— Mean, with 95 pct confidence interval, tree diameter by species for trees with a) natural and b) excavated cavities. Diameter classes are based on the relative number of cavities. Starts indicate incomplete excavations.

deciduous and evergreen oaks are important to meet the needs of primary cavity nesters for nest substrates and secondary cavity nesters for natural and excavated cavities.

## *Acorn Woodpecker Granary Trees*

Acorn woodpeckers, cooperative breeders, spend considerable time storing acorns in small excavations in tree boles and limbs. The quantity and quality of stored acorns apparently have an influence on clutch size, reproductive success, group size, group composition, and winter survivorship (Koenig and Mumme 1987). Comparing use versus availability of each tree species for acorn storage, we found use to be significantly different than availability for both minor ($X^2 = 90$, df = 4, $p < 0.001$) and major granary trees ($X^2 = 62$, df = 4, $p < 0.001$). White oaks were used as both minor and major granary trees significantly greater than expected. White oaks comprised approximately 10 percent of all trees, and yet over 25 percent of the minor granary trees and almost 50 percent of the major granary trees occurred in white oaks.

Blue oaks were used extensively as minor and major granary trees, but significantly less than expected. Although the use of blue oaks as granary trees was less than their availability (70 percent), blue oaks still provided over half of the trees used for acorn storage. All other trees species comprised a relatively small proportion of the available trees and were used equal to or less than their availability.

The DBH of granary trees were significantly (F = 189, df = 2, p < 0.001) larger than those of non-granary trees (fig. 9b). The differential use of larger diameter trees for granaries was not consistent across all tree species. Only white, blue, and black oak granary trees were significantly larger than non-granary trees.

The almost exclusive use of deciduous oak trees greater than 75 cm in diameter for major granary trees is an important management consideration. The ability of an oak woodland to support acorn woodpeckers depends on the availability of storage trees and acorns. Our data provide additional support for the need for large diameter trees for acorn storage.

Maintenance of large diameter oak trees of a variety of species is also an important component of providing an adequate supply of acorns for acorn woodpeckers. Large diameter trees produce greater quantities of acorns, and each species of oak has unique responses to environmental conditions and unique acorn characteristics (Koenig and Mumme 1987). Maintenance of a variety of oak species will help ensure that at any one point in time the environmental conditions will be favorable for the production of acorns by one or more species of oak.

### *Effects of Plot Size on Bird Community Patterns*

Each study plot was selected to be homogeneous in tree density and spatial arrangement of trees, but to vary in these characteristics among plots. Given this study design, we were surprised to find so few bird species associated with variation in tree density. We believe our plots were representative, however, of the inherent variation in oak woodlands in our study area, at least at the scale of 5 ha sample units. The study area was heterogeneous in tree structure and composition, and the spatial pattern of the vegetation. There were few discrete boundaries separating the various vegetation patches. Because of the heterogeneity of northern oak woodlands, we were uncertain as to the correct spatial scale for sampling and analysis to characterize bird community patterns. In an attempt to gain insight into this question, we analyzed the influence of increasing plot size on among-plot variation in canopy closure (a correlate of tree density), using each 5 ha study plot as a nucleus for plots of increasing size up to 50 ha. The among-plot variation in canopy closure decreased as plot size increased, but remained high even with 50 ha plots. This pattern suggests that bird community studies` may require plots in excess of 50 ha to represent the inherent variation in tree density, canopy closure, and spatial pattern of trees representative of oak woodlands in our study area. This approach could be taken with other vegetation variables to estimate the plot size at which among-plot variation is acceptably low. Large study plots, however, increase the difficulty of spatial replication.

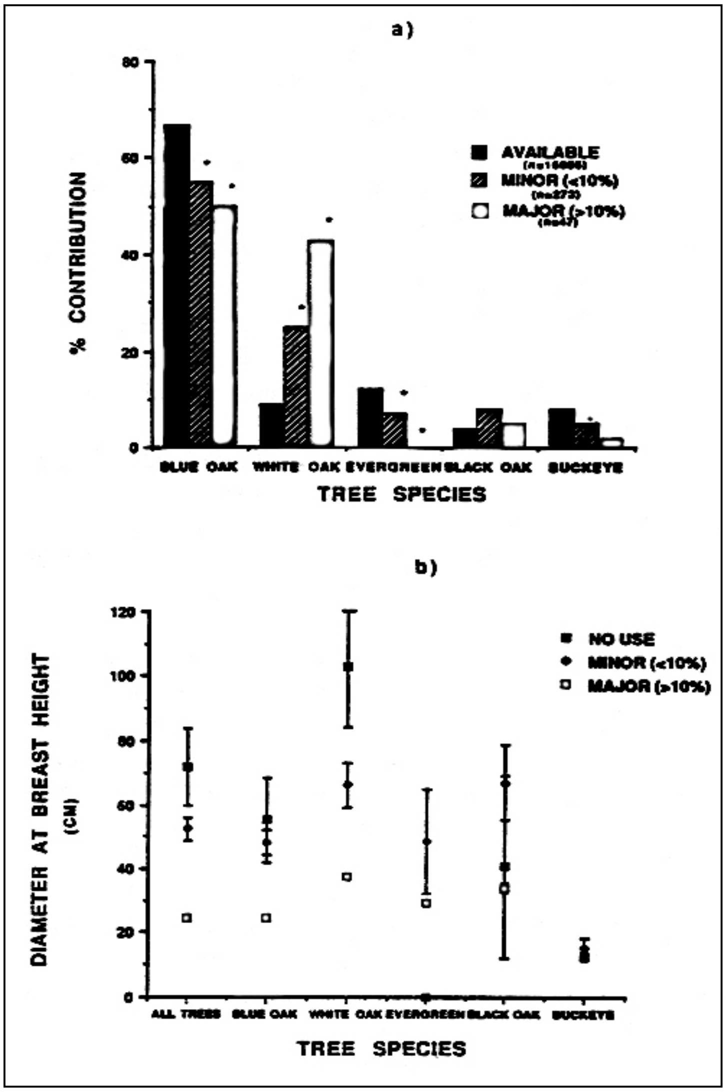


**Figure 9—Characteristics of granary trees created by acorn woodpeckers: a) tree species used for granaries compared to tree species availability (* Indicates p < 0.05); b) mean, and 95% confidence interval, tree diameter by species. Diameter classes are based on the relative number of cavities.**

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## CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

(1) Cavity-nesting species comprised a significant proportion of the breeding species and the majority of the breeding density. Thus, this guild deserves special consideration in any management decisions.

(2) The cavity-nesting guild used a variety of tree species for nest sites. This suggests that maintaining a high tree species richness, as alternative substrates for nesting, is important for this guild of breeding birds.

(3) The acorn woodpecker plays a key role in the cavity-nesting guild. This species is the primary source of excavated cavities for the secondary cavity-nesting species. We recommend maintaining large (> 50 cm DBH) blue and valley oaks, particularly those with some degree of decadence.

(4) Plain titmouse and white-breasted nuthatch nested primarily in natural cavities. These cavities result from injury to the tree followed by diseases which soften heartwood. Trees with these characteristics should be maintained as they are important to both primary and secondary cavity-nesters.

(5) The large (>75 cm DBH) deciduous oaks are particularly important as sites for acorn woodpecker granary trees. We recommend maintaining large valley and blue oak trees whenever possible.

(6) The abundance of the most common breeding species covaried with a large number of vegetation variables. Among these were seven species of hardwood trees. These results suggest that a high tree species richness is important to oak woodland birds, perhaps as alternative substrates for nesting and foraging.

(7) The abundance of some of the most common and least common breeding species covaried with tree density, both positively and negatively. To maintain the integrity of the breeding bird community, we recommend maintaining a variety of tree densities. In general, however, we failed to find a significant association between bird abundance and variation in tree density.

(8) Oak woodlands are very diverse in terms of the spatial distributions of their trees. Our data suggest that bird species respond to this variation at a variety of spatial scales. We recommend that oak woodlands be managed at large spatial scales. Until better data are forthcoming, we tentatively recommend 50-100 ha as the minimum size of a management unit.

(9) Given the spatial scale of our study (5-10 ha plots) and the spatial scale at which plots had homogenous canopy closure (~50 ha), we tentatively recommend that future community studies of oak woodland birds be done on large plots.

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