SILVICULTURAL OPTIONS IN MANAGED OAK WOODLANDS

TO BENEFIT BREEDING BIRDS

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Barry R. Noon, Ph.D.
Patricia N. Manley
Randolph A. Wilson

Department of Wildlife
Humboldt State University
Arcata, California 95521

INTRODUCTION

Approximately eight million hectares in California, or 20 percent of the state's land area, are vegetated by one or more species of oak. Trends in the harvest of oak trees in California are increasing rapidly; fuelwood harvest has increased steadily since 1959, turning sharply upward in 1973 (Menke and Fry 1980, Walt et al. 1985). Oaks are a source of quality fuelwood and are currently of high commercial value. In addition, the rate of conversion of oak woodlands to non-forest habitat types for residential and commercial development has also increased markedly since 1973 (Bolsinger 1987). However, the harvest of oaks may preclude or severely reduce the value of land for wild and domestic animals. In addition, oaks provide aesthetic benefits that are important in the California landscape (Litton 1980, Johnson 1987, Pillsbury and Oxford 1987). As a consequence, there is a contrast and potential conflict in the demand for oaks.

Oak woodlands in California face other threats in addition to exploitation for fuel wood. Most oak habitats are characterized by very poor regeneration and extremely low seedling and sapling survival. The exact cause for the low recruitment is controversial 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). However, recent research indicates that the agents limiting regeneration differ with tree species and site (Bartolome et al. 1987, Muick and Bartolome 1987). Combining the negative effects of exploitation for fuel wood and poor regeneration points out the immediate threats faced by California oak habitats.

In the face of these threats and the increasing trend of exploitation, it is particularly disturbing to discover that very little is known about the relationship between California wildlife and oak woodlands. Muick and Bartolome's (1985) listing of California oak studies included only 16 bird studies, 15 mammal studies, and one reptile and amphibian study conducted between 1953 and 1985. Few of these studies addressed the results of habitat disturbance on the wildlife community. Ohmann and Mayer (1987) reported that over 300 wildlife species found hardwood habitats to be optimum or suitable for reproduction, according to a query of the California Wildlife Habitat Relationships data base. Barrett (1980) indicated that over 100 mammal species in California utilize oak habitats and listed several of California's most important game species as consumers of oak browse and acorns. Over much of their range the density of game species such as deer, bear, pig, and squirrel fluctuate in synchrony with the annual acorn mast crop suggesting that they are limited by this resource (Barrett 1980). Despite this apparent dependence, there are no published studies documenting the effect of removing oaks from preferred habitats on resident mammal populations.

Approximately 110 species of birds can be observed during the breeding season in California oak habitats (Verner 1980). Verner (1983) showed that "oak woodlands rank among the top three habitat types in the number of bird species for which they provide breeding habitat." Birds utilize oaks for perching, feeding, and nesting. Large, old trees are particularly important to birds because they offer numerous feeding sites, produce more acorns, and are best suited to excavation by cavity nesters (Verner 1980). As with mammals, Verner has reported that our knowledge of avian species is very limited. Few systematic studies have been conducted on the effects of birds on California oaks. As an example of their impact, it is known that birds may remove much of the maturing acorn crop from oak woodlands (Griffin 1980). The most effective predators are Acorn Woodpeckers (Melanerpes formicivorous), Scrub and Steller's Jays (Aphelocoma coerulescens and Cyanocitta stelleri, respectively), and Yellow-billed Magpies (Pica nuttali). The jays and magpies bury large numbers of acorns, many of which are not recovered and may later germinate. Thus birds may play a significant role as vectors of seed dispersal and aid the regeneration of these woodlands. Birds also consume insects which damage trees and, as a result, be effective at preventing serious outbreaks of defoliating insects. Birds may also have deleterious effects on the trees, such as dispersal of mistletoe berries through their feces and the excavation of holes for nesting and feeding, which may increase the tree's vulnerability to invasion by insects or pathogens.

Providing for birds in managed oak woodlands will require that sufficient numbers of trees be available to meet the nesting, feeding, and cover requirements of the birds in the community (Verner 1980). Especially important may be the availability of acorns. Wildlife in California oak habitats has been observed to remove all acorns from traps even in years of heavy mast production (Griffin 1976) suggesting that this resource may limit their populations. For example, the reproductive success of Acorn woodpeckers varied positively with the abundance, and quality of the acorn crop stored for a population of Acorn woodpeckers at Hastings Reservation, California (Koenig and Mumme 1987:98). However 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 disturbance of these habitats. For example, at this time it is impossible to make any statement about what residual density of trees is required to meet the needs of the bird community on managed woodlands. It is important that the needs of the wildlife community be considered along with economic and aesthetic perspectives in the management of California's oak woodlands.

STUDY OBJECTIVES

In the exploitation of California oak woodlands for fuel wood two silvicultural options which can easily be targeted for management are (1) the residual density of trees remaining after the harvest, and (2) given a specific residual tree density, the spatial distribution of the remaining trees in the landscape. These two factors, tree density and spatial distribution, can be optimized for a variety of purposes including regeneration potential, forage production, aesthetic quality, and wildlife value.

In this paper we report on the relationship among various attributes of the breeding bird community and varying tree density. The relationship of the bird community to the vegetative community is defined by (1) changes in bird species composition, (2) changes in the abundance of particular bird species, (3) changes in the distribution of bird species, and (4) changes in total avian density or biomass.

An additional objective was to explore the relationships of the bird community to variation in aspects of the vegetative community other than tree density. Specifically, we explore how abundance of individual species and species groups covaries with changes in tree and shrub species and with changes in vegetative structure.

As a final objective we described the nest site selection patterns of the cavity nesting birds. Selection was explored in terms of used and available tree species and in terms of each bird species' pattern of tree selection.

STUDY AREA

The study area was located at the University of California Hopland Field Station five miles east of Hopland, in Mendocino County, California (Fig. 1). The study area was located near the northern limit of blue oak woodlands in the Coastal Range (Fig. 2). The dominant vegetation of the study area was described as the blue oak (Quercus douglasii) phase of the Coast Range foothill woodland (Griffin 1977). Blue oak was the dominant tree species throughout the field station. It was found in association with valley oak (Q. lobata), interior live oak (Q. wislizenii), California black oak (Q. kellogii), Oregon white oak (Q. garryana), California bay (Umbellularia californica), and buckeye (Aesculus californica). Annual grasses and forbs dominated the ground cover. Density of tree cover varied and was controlled by local site conditions as well as past disturbance history. Adjacent vegetation types included chapparal, mixed hardwood and conifer forest, and meadows. Sheep grazing was the primary land use. Portions of the area, however, were retained as biological reserves (sheep and/or deer grazing were excluded). Woodcutting was allowed to a limited degree.

The topography of the area 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 of the field station 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. The climate was Mediterranean

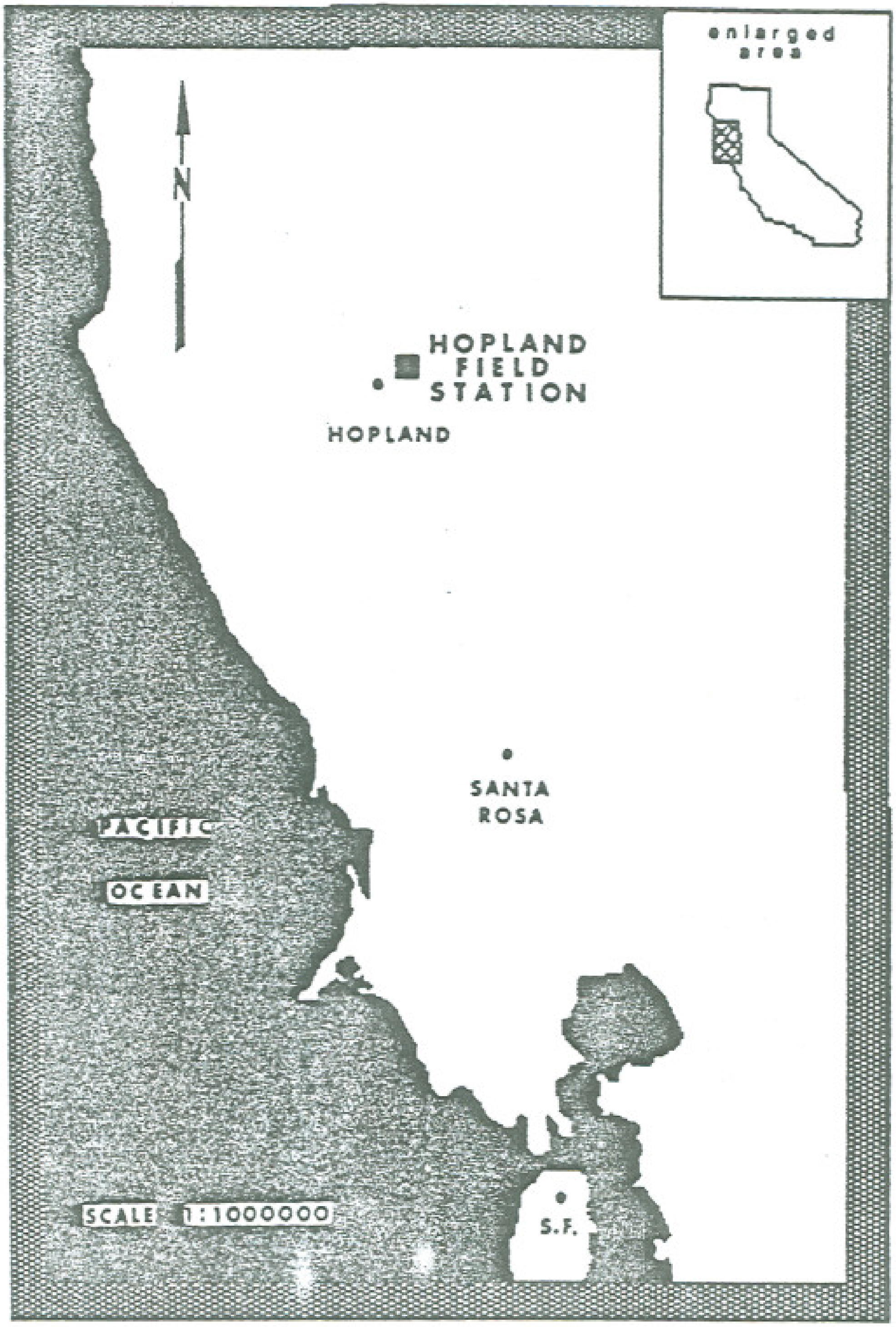


Figure 1. Location of the study area at the University of California Hopland Field Station. The field station is located 8 km east of Hopland, in Mendocino County, California.

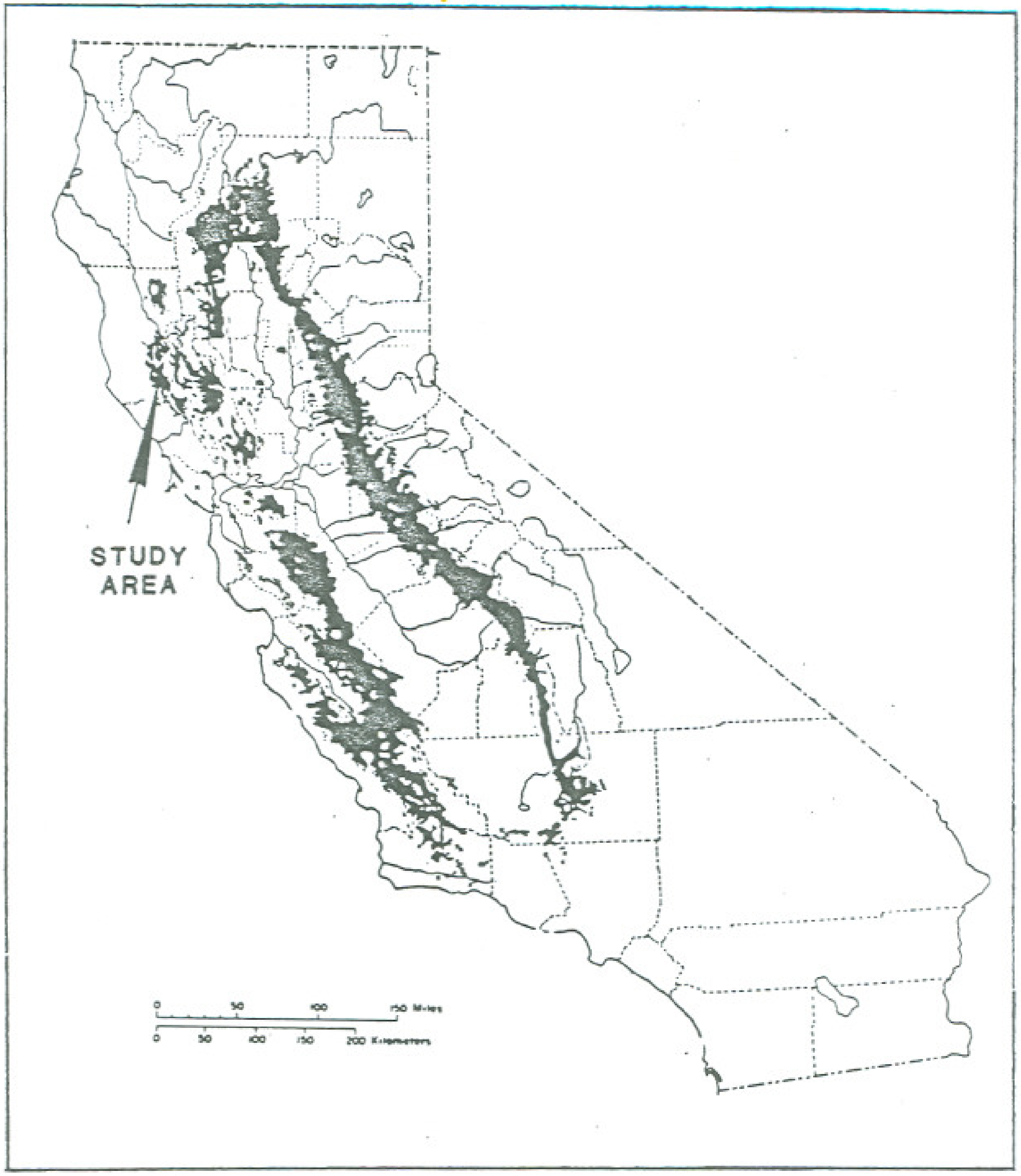


Figure 2. Distribution of blue oaks (Quercus douglassii) in California (from Griffin and Critchfield 1972). Shaded areas indicate stands of trees over two miles in diameter. Small x's indicate stands less than two miles across or of unknown size.

(Griffin 1977). Average annual rainfall was 90 cm occurring between September and June. Average summer and fall temperatures ranged from 20-25 degrees centigrade (Pitt 1975). Winters were mild with some frost in the valleys and infrequent, light snow at higher elevations.

METHODS

Study Plots

Twenty-three, 5 ha (100 x 500 m) study plots were established throughout the continuum of available tree densities within blue oak habitats. Blue oak habitats were defined as areas in which the proportion of the total tree density was greatest for blue oaks. Uniform tree density and distribution within and adjacent to (within 50 m of plot boundries) plots were important criterion for plot placement in order to reduce within plot variation and the effect of dissimilar adjacent vegetation. 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 2,143 ha study area. Wooden stakes (1"x 3"x 5') spaced 50 m apart delineated a center transect line through each plot and 50 m reference points on either side. The stakes were numbered and lettered to indicate their location within the plot.

Censusing

A modified spot-mapping method was used to describe species composition, abundance, density, and dispersion of the bird community on each study plot (International Bird Census Committee 1969, Emlen 1977, Christman 1984). Each plot was censused once per week between late March and mid June during 1986 and 1987 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 the 100 m on either side of the transect line and within 25 m of either end. The rectangular shape of the plots increased the amount of edge and therefore the number of partial territories overlapping plot boundries. Partial territories generally decrease the accuracy of territory density estimates in conventional spot-mapping (Marchant 1980). To reduce the possible bias introduced by partial territories, we censused birds out to 100 m on either side of the transect line and 25 m on either end of each plot. This "buffer area" around each plot increased the effective size of the censused area to 11 ha. Howver, analysis of avian densities and abundances are based on estimates from the central 5 ha (100 m X 500 m) of the plot.

Each census required one hour to complete. We rigorously adhered to the fixed duration of each census. The pace of the census was based on those conditions, high density vegetation and abundant birds, requiring the most observer effort. This time period ensured an adequate amount of time to detect birds and accurately map their locations. Therefore, our slow pace reduced detection differences that might occur due to differences in vegetation density. A total of four different individuals were involved in collecting the census data; two collected data in both years.

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. We assumed that the detection probabilities were variable between bird species but equal for each species across plots out to 50 m on either side of the transect line. Detection probabilities within species were assumed to be consistent across all study plots because of the openess of the habitat and the slow pace of the census. In addition, we attempted to keep double counting of birds to a minimum and we believe double counting occurred infrequently.

Tree Use By Cavity Nesting Birds

Cavity nesting species comprise a large percent of the bird biomass in oak woodlands (Verner 1980). Because of the importance of this group in oak woodlands, we investigated in more detail the characteristics of the vegetation that might be important to their needs, especially in regards to nesting requirements. Questions addressed with regard to the cavity nesting species included: 1) For all cavity trees, was there a relationship between tree size and numbers of cavities? 2) What tree species were chosen for nest sites, and were these choices in proportion to tree species availability? 3) Given that acorn storage trees were a critical resource to Acorn woodpeckers, what tree species were selected and what characteristics about these trees made them desirable. 4) Were natural cavities distributed randomly among tree species or did certain species characteristically contain more than others? 5) Was there potential for certain cavity nesting species to compete for cavities or was there clear separation in the choice of tree species and cavity type?"

Nest Search

During the spring of 1986, we attempted to locate as many nests as possible of all breeding species in order to verify the breeding status of each species and to verify the location of mapped territories. During 1987, our efforts were focused on cavity nesting species, though nests of any bird species encountered were recorded and described. Nests were located opportunistically and by active search. We looked for birds carrying nest materials or food and followed these birds, when possible, to their nest sites.

Vegetation Measurements

The vegetation on each plot was decribed by mapping the location and recording descriptive information on each individual woody plant. The following information was recorded: plant species, total height, height of canopy above the ground, canopy radius, number of stems with a diameter at breast height (DBH) greater than 5 cm and their DBH, branching pattern (Pillsbury and Stephens 1978:12), canopy density, vigor (Thomas 1979:64), number of natural and excavated cavities, use as a granary tree, and other signs of use by wildlife.

Total tree height was measured primarily by ocular estimation and then height to the bottom of the canopy was estimated. The tree height estimations were based on frequent measurements taken with a clinometer. DBH was measured with a DBH tape. Branching pattern, canopy radius, and canopy density were visually estimated as an index to foliage density. Branching pattern (1-3, 4, or 5) categorized the canopy into three general shapes (inverted triangle, one-half ellipsiod, or ellipsoid, respectively). Canopy radius was the horizontal distance from the trunk to the edge of the canopy at either the top, middle, or bottom of the canopy, depending upon the shape of the canopy (inverted triangle, ellipsoid, or one-half ellipsiod, respectively). To index canopy foliage density, canopies were categorized as less than one-third occupied, one-third to two-thirds occupied, and greater than two-thirds occupied by leaves.

Trees with natural and/or excavated cavities were each categorized as containing 0, 1-3, or >3 cavities. The suitability of cavities for bird use was not determined. Cavities were counted when the entrance appeared of suitable dimension for use by cavity nesting birds. Our aim was to describe relative abundance of cavities between plots. A tree's use as an Acorn woodpecker granary tree was categorized as: no evidence, <10 percent, or >10 percent used for storage. Six individuals were involved in collecting the vegetation data and all measurements and visual estimates occurred within a four month period. Rigorous training occurred before and during the field work to reduce variability within and among observers for measured and estimated parameters.

Data Analysis

Univariate Analyses. -- Preliminary descriptive analyses were performed to review distributions of individual variables and relationships between variables. Histograms were used to assess the normality of distributions and deviations were corrected by appropriate transformations. Bivariate scattergrams and correlation coefficients were evaluated to discern relationships among variables.

Data collected from all 23 plots were used in the following analyses. To test the hypothesis of no relationship between tree size (DBH) and number of cavities, analysis of variance (ANOVA) was performed separately for each tree species, and for all tree species combined. The tree diameter data were grouped by cavity category for analysis. Prior to the ANOVA, tree diameter data were transformed (square root or fourth root) to increase their fit to a normal distribution and to decrease the variance among groups. However, for graphic presentation, confidence intervals and means were expressed using the untransformed data. If a significant ANOVA resulted, Tukey tests were used for all possible two way comparisons. A similar set of ANOVAs were done to test the hypothesis of no relationship between tree size and acorn storage use by Acorn woodpeckers.

We used the Chi-square goodness-of-fit statistic to test the hypothesis that trees with natural and excavated cavities were used in proportions equal to their occurrence in the population. To test the hypothesis, by individual tree species, we used Bonferroni's normal statistic (Neu et al. 1984). This statistical technique compares the percent use to the percent occurrence in the population after adjusting each test to maintain a constant experimentwise error rate $\leq$ 0.05. The same statistical procedure was also used to test: (1) whether certain tree species were chosen for acorn storage disproportionate to their availability; and (2) the hypothesis that cavity nesters were chosing certain tree species for nest sites equal to that expected by tree species availability. Because of small sample sizes, only natural cavity selection by Plain titmouse and White-breasted nuthatch were analyzed in this way. Although tree selection for other cavity nesting species is presented, no statistical significance can be assigned to the observed results. Departures of observed from expected frequencies were considered significant at alpha $\leq$ 0.05 for all tests.

Multivariate Analyses. -- We estimated the value of a large number of structural and floristic vegetation variables, many of which were highly redundant. In order to simplify these data, but retain most of their information, we performed a series of data reduction steps. First, we greatly reduced the dimensionality of our data by grouping variables on the basis of the absolute value of their correlation coefficients. We retained for subsequent analysis at most two variables from each of these groups. Second, we selected for retention those vegetative variables which were easiest to discuss with land managers and of most relevance to those making land use decisions. The first and second steps were often considered simultaneously.

To estimate the major axes of vegetative variation, we extracted the dominant components from the correlation matrix (based on the reduced number of variables) of vegetative variables by principal components analysis (PCA). Subsequent to estimating these principal components, we performed a varimax rotation and then ordinated each of the 23 vegetation samples (i.e. study plots) by their standardized factor scores. The biological interpretation of the principal components was based on their factor loadings which are simple correlations between the component scores and the original variables.

A similar approach was taken to estimate the major axes of variation in the bird community. Bird species can be grouped by their degree of ecological similarity on the basis of one or more criteria; for example, foraging substrate or nest site selection. The bird species detected during censusing were grouped into nine overlapping groups based on foraging behavior, nest site, and habitat association (Table 4). The bird groups and their associations are: (1) primary cavity nesters, bird species that excavate and nest in nest holes; (2) secondary cavity nesters, bird species that nest in cavities but do not excavate nest holes; (3) bark foragers, bird species which forage primarily on bark (trunks and branches) dwelling prey; (4) air salliers, bird species which forage primarily on flying insects; (5) ground foragers, bird species which obtain prey primarily from the ground; (6) foliage foragers, bird species which obtain prey primarily from foliage; (7) conifer habitat associates, bird species which are found in greatest abundance in coniferous forests in the Pacific northwest; (8) winter residents, bird species which winter in our study area and breed in other habitats; and (9) migrants, bird species which passed through our study area during early spring but did not breed.

The abundance of individuals in each of the nine groups was estimated for each plot. Next, we estimated the dominant components from the correlation matrix of the bird group abundances using PCA. As described for the PCA of vegetative data, we performed a varimax rotation, ordinated each of the 23 samples (i.e. study plots) by their standardized scores, and then interpreted the principal components based on their factor loadings.

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

All possible subsets regression was used to select a "best" subset of vegetative variables (independent variables) to explain variation in a number of possible dependent variables. The dependent variables were those variables that described different aspects of the bird community abundances or of individual species (average number of detections / census). All possible subsets regression using Mallow's Cp criterion was chosen because it provides a "best" subset which minimizes the total mean squared error of fitted values (Neter et al. 1985:421).

The independent variables available for selection in the regression analyses were those which best described the overall structural and floristic characteristics of the plots. Care was taken to use variables which described an entire resource (e.g. total number of blue oak trees) versus portions of a resource (e.g. number of blue oak trees in DBH intervals) to minimize the amount of correlation between independent variables. The tolerance limit for the largest multiple correlation was set at 0.01 to maximize the accuracy of the inverted cross-products matrix.

Histograms of independent and dependent variables were visually evaluated and revealed that many of the variables (count data) were positively skewed. Square root transformations of count data and arcsine transformation of percentage variables (Sokal and Rohlf 1981:421,427) were used to improve fit to normal distributions.

RESULTS

Description of the Bird Community

Territory sizes were too large and detections too few to enable the use of Christman's (1984) method of territory estimation for most bird species. However, since the censuses were rigorously timed, we treated each census as a fixed width (50 m on each side) belt-transect and used the mean number of detections per census per species as our dependent variable. These estimates were used to characterize the species abundance distribution for each plot.

We were able to calculate territory density using Christman's (1984) method for the Plain titmouse (Parus inornatus). A comparison of territory density and the mean number of detections per census showed that, for Plain titmouse, the two methods were highly correlated ($r = 0.86$, $p < 0.01$, Fig. 3). Therefore, the less time intensive belt-transect census method may be an acceptable alternative to the spot-mapping method, at least for the Plain titmouse.

Ninety-three bird species were observed on the field station between January 1986 and September 1987 (Table 1). Seventy-two bird species were detected during censusing. The abundances of all bird species detected over all study plots are given in Table 1. Fourty-nine bird species were observed in territorial behaviors and presumed breeding on the study plots. The ten most abundant bird species over all plots are listed in Table 2. Note that of these 10, six are cavity nesting species. Cavity nesters comprised 24.5 percent (12 species) of the breeding bird species and 58.1 percent of breeding

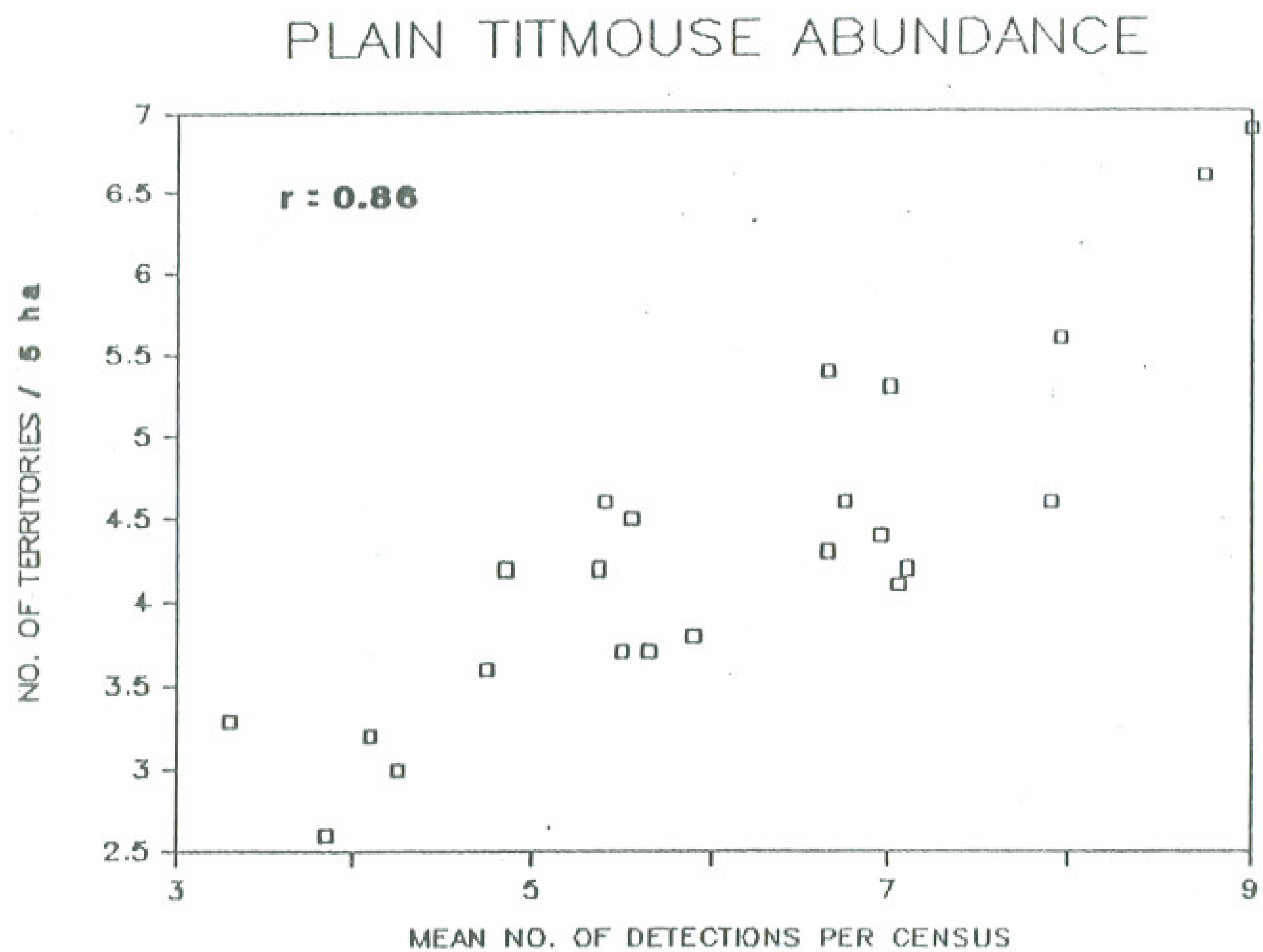


Figure 3. Bivariate scattergram of number of territories per plot and mean number of detections per census per plot for the Plain titmouse.

Table 1. List of bird species at the U.C. Davis Hopland Field Station. The residency status (RES. CODES), number of nests located, frequency of occurrence (% FREQ), mean density, and standard error of the mean (S.E.), across all study plots are listed for each bird species. Data were collected during the breeding seasons (March-June) of 1986 and 1987. Bird species are listed in taxonomic order.

RESIDENCE CODES: 1) year round resident; 2) winter resident; 3) spring/summer resident; 4) migrant, spring or fall

MNEMONIC	SPECIES	RES. CODE	NESTS	% FREQ	x BIRDS PER 40ha	S.E.
WODU	Wood Duck (Aix sponsa)	1	0	0	n.d.	
MALL	Mallard (Anas platyrhynchos)	1	0	4	< 0.1	< 0.1
TUVU	Turkey Vulture (Cathartes aura)	1	0	43	0.4	0.1
BSKI	Black-shouldered Kite (Elanus caeruleus)	1	0	0	n.d.	
SSHA	Sharp-shinned Hawk (Accipiter striatus)	1	0	0	n.d.	
COHA	Cooper's Hawk (Accipiter cooperii)	1	0	17	0.1	< 0.1
NOGO	Northern Goshawk (Accipiter gentilis)	4	0	0	n.d.	
RSHA	Red-shouldered Hawk (Buteo lineatus)	1	0	17	0.1	< 0.1
RTHA	Red-tailed Hawk (Buteo jamaicensis)	1	3	48	0.4	0.1
GOEA	Golden Eagle (Aquila chrysaetos)	1	3	26	< 0.1	< 0.1
AMKE	American Kestrel (Falco sparverius)	1	2	35	0.4	0.1
PEFA	Peregrine Falcon (Falco peregrinus)	3	0	0	n.d.	
BLGR	Blue Grouse (Dendragapus obscurus)	4	0	0	n.d.	
WITU	Wild Turkey (Meleagris gallopavo)	1	2	17	0.2	0.1
CAQU	California Quail (Callipepla californica)	1	3	85	5.4	0.7
MOQU	Mountain Quail (Oreortyx pictus)	1	0	30	0.7	0.2
AMCO	American Coot (Fulica americana)	1	0	0	n.d.	
KILL	Killdeer (Charadrius vociferus)	1	0	0	n.d.	
BTPI	Band-tailed Pigeon (Columba fasciata)	2	0	61	52.8	24.7

Table 1 cont.

MNEMONIC	SPECIES	RES. CODE	NESTS	% FREQ	x BIRDS PER 40ha	S.E.
MODO	Mourning Dove (*Zenaida macroura*)	1	15	100	10.4	0.6
WSOW	Western Screech-owl (*Otus kennicottii*)	1	0	0	n.d.	
GHOW	Great Horned Owl (*Bubo virginianus*)	1	0	0	n.d.	
BAOW	Barn Owl (*Tyto alba*)	1	1	0	n.d.	
NPOW	Northern Pygmy-owl (*Glaucidium gnoma*)	1	0	30	0.4	0.1
ANHU	Anna's Hummingbird (*Calypte anna*)	1	0	96	2.2	0.2
RUHU	Rufous Hummingbird (*Selsphorus rufus*)	4	0	0	n.d.	
ALHU	Allen's Hummingbird (*Selasphorus sasin*)	4	0	0	n.d.	
LEWO	Lewis' Woodpecker (*Melanerpes lewis*)	2	0	0	n.d.	
ACWO	Acorn Woodpecker (*Melanerpes formicivorus*)	1	29	100	25.4	1.2
RBSA	Red-breasted Sapsucker (*Sphyrapicus ruber*)	2	0	0	n.d.	
NUWO	Nuttall's Woodpecker (*Picoides nuttallii*)	1	12	96	5.8	0.4
DOWO	Downy Woodpecker (*Picoides pubescens*)	1	0	30	0.1	< 0.1
HAWO	Hairy Woodpecker (*Picoides villosus*)	1	0	0	n.d.	
NOFL	Northern Flicker (*Colaptes auratus*)	1	3	70	1.2	0.2
PIWO	Pileated Woodpecker (*Dryocopus pileatus*)	1	0	0	n.d.	
OSFL	Olive-sided Flycatcher (*Contopus borealis*)	4	0	0	n.d.	
WWPE	Western Wood-pewee (*Contopus sordidulus*)	3	3	39	1.1	0.2
WEFL	Western Flycatcher (*Empidonax difficilis*)	3	0	91	1.8	0.2
BLPH	Black Phoebe (*Sayornis nigricans*)	1	1	22	0.1	< 0.1
ATFL	Ash-throated Flycatcher (*Myiarchus cinerascens*)	3	0	96	3.4	0.3
WEKI	Western Kingbird (*Tyrannus verticalis*)	3	3	65	1.5	0.2
TRSW	Tree Swallow (*Tachycineta bicolor*)	3	1	9	0.1	< 0.1
VGSW	Violet-green Swallow (*Tachycineta thalassina*)	3	20	100	58.4	2.3

Table 1 cont.

MNEMONIC	SPECIES	RES. CODE	NESTS	% FREQ	x BIRDS PER 40ha	S.E.
RWSW	Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	4	0	0	n.d.	
STJA	Steller's Jay (*Cyanocitta stelleri*)	1	0	96	5.3	0.4
SCJA	Scrub Jay (*Aphelocoma coerulescens*)	1	2	100	11.0	0.6
AMCR	American Crow (*Corvus brachyrhynchos*)	1	0	13	0.1	0.1
CORA	Common Raven (*Corvus corax*)	1	0	17	0.1	< 0.1
PLTI	Plain Titmouse (*Parus inornatus*)	1	112	100	48.8	1.6
BUSH	Bushtit (*Psaltriparus minimus*)	1	7	100	6.1	0.5
WBNU	White-breasted Nuthatch (*Sitta carolinensis*)	1	45	100	13.5	0.6
BRCR	Brown Creeper (*Certhia americana*)	1	8	100	4.6	0.5
BEWR	Bewick's Wren (*Thryomanes bewickii*)	1	0	26	0.2	< 0.1
HOWR	House Wren (*Troglodytes aedon*)	3	1	22	0.4	0.1
RCKI	Ruby-crowned Kinglet (*Regulus calendula*)	2	0	87	1.1	0.2
BGGN	Blue-gray Gnatcatcher (*Polioptila caerulea*)	3	6	74	2.8	0.3
WEBL	Western Bluebird (*Sialia mexicana*)	1	39	100	10.0	0.6
HETH	Hermit Thrush (*Catharus guttatus*)	2	0	26	0.1	< 0.1
AMRO	American Robin (*Turdus migratorius*)	1	9	100	16.2	0.8
VATH	Varied Thrush (*Ixoreus naevius*)	2	0	35	< 0.1	< 0.1
WREN	Wrentit (*Chamaea fasciata*)	1	0	4	< 0.1	< 0.1
CATH	California Thrasher (*Toxostoma redivivum*)	1	0	0	n.d.	
CEWA	Cedar Waxwing (*Bombycilla cedrorum*)	2	0	4	< 0.1	< 0.1
EUST	European Starling (*Sturnus vulgaris*)	1	24	87	10.2	0.9
SOVI	Solitary Vireo (*Vireo solitarius*)	3	5	83	4.0	0.4
HUVI	Hutton's Vireo (*Vireo huttoni*)	1	4	91	2.6	0.2
WAVI	Warbling Vireo (*Vireo givus*)	3	0	74	1.6	0.2

Table 1 cont.

MNEMONIC	SPECIES	RES. CODES	NESTS	% FREQ	BIRDS PER 40ha	S.E.
OCWA	Orange-crowned Warbler (*Vermivora celata*)	3	1	100	5.3	0.4
NAWA	Nashville Warbler (*Vermivora ruficapilla*)	4	0	0	n.d.	
YEWA	Yellow Warbler (*Dendroica petechia*)	4	0	9	0.1	0.1
YRWA	Yellow-rumped Warbler (*Dendroica coronata*)	4	1	78	2.8	0.4
BGWA	Black-throated Gray Warbler (*Dendroica nigrescens*)	4	0	70	1.3	0.2
TOWA	Townsend's Warbler (*Dendroica townsendi*)	4	0	43	0.5	0.1
HEWA	Hermit Warbler (*Dendroica occidentalis*)	4	0	48	0.6	0.2
WIWA	Wilson's Warbler (*Wilsonia pusilla*)	4	0	83	1.1	0.2
WETA	Western Tanager (*Piranga ludoviciana*)	3	0	78	1.9	0.2
BHGR	Black-headed Grosbeak (*Pheucticus melanocephalus*)	3	6	83	3.5	0.4
RSTO	Rufous-sided Towhee (*Pipilo erythrophthalmus*)	1	0	43	0.5	0.1
BRTO	Brown Towhee (*Pipilo fuscus*)	1	2	96	3.4	0.3
CHSP	Chipping Sparrow (*Spizella passerina*)	3	4	83	5.6	0.5
LASP	Lark Sparrow (*Chondestes grammacus*)	1	7	78	5.8	0.5
GCSP	Golden-crowned Sparrow (*Zonotrichia atricapilla*)	2	0	13	0.2	0.1
WCSP	White-crowned Sparrow (*Zonotrichia leucophrys*)	1	0	9	0.2	0.1
DEJU	Dark-eyed Junco (*Junco hyemalis*)	1	2	100	9.4	0.9
RWBL	Red-winged Blackbird (*Agelaius phoeniceus*)	1	0	30	0.6	0.2
WEME	Western Meadowlark (*Sturnella neglecta*)	1	0	65	1.3	0.2
BRBL	Brewer's Blackbird (*Euphagus cyanocephalus*)	1	0	57	1.5	0.3
BHCO	Brown-headed Cowbird (*Molothrus ater*)	3	0	78	1.3	0.2
NOOR	Northern Oriole (*Icterus galbula bullockii*)	3	6	96	3.6	0.3
PUFI	Purple Finch (*Carpodacus purpureus*)	2	0	83	3.2	0.7
HOFI	House Finch (*Carpodacus mexicanus*)	1	2	83	2.4	0.4

Table 1 cont.

MNEMONIC	SPECIES	RES. CODES	NESTS	% FREQ	BIRDS PER 40ha	S.E.
PISI	Pine Siskin (*Carduelis pinus*)	2	0	4	< 0.1	< 0.1
LEGO	Lesser Goldfinch (*Carduelis psaltria*)	1	18	100	20.6	1.1
LAGO	Lawrence's Goldfinch (*Carduelis lawrencei*)	1	0	17	0.8	0.3

a/ The density of bird species detected on the station but not during censusing is denoted with n.d. (no detections).

Table 2. Ten most abundant breeding bird species across all study plots. Abundance estimates reflect the mean number of detections per species over all plots (1986-1987).

SPECIES	BIRDS/40 HA
VIOLET-GREEN SWALLOW	58.4
PLAIN TITMOUSE	48.8
ACORN WOODPECKER	25.4
LESSER GOLDFINCH	20.6
AMERICAN ROBIN	16.2
WHITE-BREASTED NUTHATCH	13.5
SCRUB JAY	11.0
MOURNING DOVE	10.4
EUROPEAN STARLING	10.2
WESTERN BLUEBIRD	10.0

individuals (Table 3). The most common cavity nesting species were Violet-green swallow, Plain titmouse, Acorn woodpecker and White-breasted nuthatch. Secondary cavity nesters alone comprised almost half (47.5 percent) of breeding individuals.

The 72 bird species detected during censusing were grouped into nine overlapping groups (Table 4). The number of species in each group ranged from three to 19, and the abundance of each species within a group ranged from 0.01 - 7.28 detections per census (Table 1).

The number of breeding species per study plots increased with elevation (Fig. 4). The change in breeding species richness with elevation was primarily attributable to the addition of more conifer-associated (Fig. 5a) and migrant (Fig 5b) species on the upper elevational plots. Changes in the number of species in these groups may have been related to vegetation changes with elevation (see below).

Multivariate Analysis of the Bird Community

PCA was performed on nine untransformed bird group abundance estimates to identify those bird groups most aligned with variation in the bird group abundance distributions among study plots. The analysis was based on the sum of the average number of detections for each species in the group. Three principal components with eigenvalues > 1.0 described 76.7 percent of the variation in bird group abundance among plots (Table 5).

Table 3. Proportion of the breeding passerine bird community comprised of cavity nesting species. Numbers are derived from census data for all 23 study plots during both breeding seasons (1986 and 1987).

NESTING GUILD	SPECIES		INDIVIDUALS	
	total # detected	% of community	x indiv per 40ha	% of community
PRIMARY CAVITY NESTERS	4	8.2	32.4	10.6
SECONDARY CAVITY NESTERS	8	16.3	145.2	47.5
ALL CAVITY NESTERS	12	24.5	177.6	58.1
ENTIRE COMMUNITY	49	100.0	305.7	100.0

Table 4. Bird groups by species composition across all plots. Mnemonic for individual bird species, mean # of detections per census, standard deviation (S.D.), range, sum, and percent contribution to the guild are listed.

MNEMONIC	MEAN	S.D.	RANGE	SUM	% CONTRIB.
PRIMARY CAVITY NESTERS					
ACWO	3.18	3.34	0-34	1453	78
NUWO	.73	1.02	0-8	334	18
NOFL	.15	.42	0-3	67	4
SECONDARY CAVITY NESTERS					
AMKE	.05	.25	0-2	23	<1
ATFL	.43	.82	0-5	197	2
EUST	1.27	2.50	0-22	581	7
HOWR	.04	.22	0-2	20	<1
PLTI	6.10	3.10	0-18	2787	33
PYOW	.05	.26	0-3	21	<1
WBNU	1.65	1.64	0-10	770	9
WEBL	1.25	1.62	0-8	572	7
VGSW	7.28	6.23	0-40	3335	40
BARK FORAGERS					
ACWO	3.18	3.34	0-34	1453	51
BRCR	.58	1.09	0-7	267	9
NUWO	.73	1.02	0-8	334	12
WBNU	1.65	1.64	0-10	770	28
AIR SALLIERS					
ATFL	.43	.82	0-5	197	5
BLPH	.01	.11	0-1	6	<1
TRSW	.01	.10	0-2	3	<1
VGSW	7.28	6.23	0-22	3335	88
WEFL	.23	.58	0-5	105	3
WEKI	.18	.63	0-6	84	2
WWPE	.14	.50	0-4	64	2

Table 4 cont.

MNEMONIC	MEAN	S.D.	RANGE	SUM	% CONTRIB.
GROUND FORAGERS					
AMRO	2.02	2.04	0-10	924	15
BHCO	.16	.52	0-5	73	1
BRBL	.19	.76	0-6	87	1
BRTO	.42	.78	0-4	194	3
CAQU	.67	1.82	0-16	307	5
CHSP	.70	1.35	0-8	319	5
DEJU	1.18	2.28	0-19	537	9
LABU	.01	.08	0-1	3	<1
LAGO	.01	.11	0-1	6	<1
LASP	.72	1.24	0-7	330	6
LEGO	2.60	2.93	0-20	1179	20
MODO	1.30	1.71	0-9	594	10
MOQU	.09	.45	0-4	40	1
NOFL	.15	.42	0-3	67	1
RSTO	.06	.33	0-3	29	<1
RWBL	.08	.56	0-9	35	1
EUST	1.27	2.50	0-22	581	10
WEBL	1.25	1.62	0-8	572	10
WEME	.16	.48	0-4	75	1
FOLIAGE FORAGERS					
BGGN	.35	.80	0-5	159	3
BHGR	.43	.95	0-6	198	4
BUSH	.75	1.26	0-6	346	7
BGWA	.17	.59	0-5	77	1
HOFI	.30	.98	0-10	138	3
HUVI	.32	.65	0-3	147	3
NOOR	.45	.88	0-5	204	4
OCWA	.66	1.13	0-8	302	6
PLTI	6.10	3.10	0-18	2787	59
SOVI	.50	.94	0-6	229	5
WAVI	.20	.58	0-5	91	2
WETA	.23	.62	0-3	106	2

Table 4 cont.

MNEMONIC	MEAN	S.D.	RANGE	SUM	% CONTRIB.
CONIFER HABITAT ASSOCIATES					
BRCR	.58	1.09	0-7	267	13
BHGR	.43	.96	0-6	198	10
BGWA	.17	.60	0-5	77	4
DEJU	1.18	2.28	0-19	537	27
SOVI	.50	.94	0-6	229	12
STJA	.66	1.12	0-6	302	15
WAVI	.20	.20	0-5	91	5
WEFL	.23	.57	0-5	105	5
WETA	.23	.62	0-3	106	5
WWPE	.14	.50	0-4	64	3
WINTER RESIDENTS					
HETH	.02	.12	0-1	7	2
PUFI	.40	1.78	0-30	180	43
RCKI	.14	.54	0-5	63	15
VATH	.02	.15	0-2	8	2
YRWA	.35	1.15	0-12	160	38
MIGRANTS					
BGWA	.17	.59	0-5	77	13
GCSP	.02	.23	0-4	9	2
HEWA	.07	.43	0-6	32	6
LEWO	.002	.06	0-1	2	<1
NAWA	.002	.05	0-1	1	<1
OSFL	.01	.09	0-1	4	<1
PISI	.004	.09	0-2	2	<1
TOWA	.06	.31	0-4	26	5
WEFL	.23	.58	0-5	105	18
WETA	.23	.62	0-3	106	18
WIWA	.13	.45	0-4	60	10
YEWA	.01	.13	0-2	4	<1
YRWA	.35	1.15	0-12	160	27

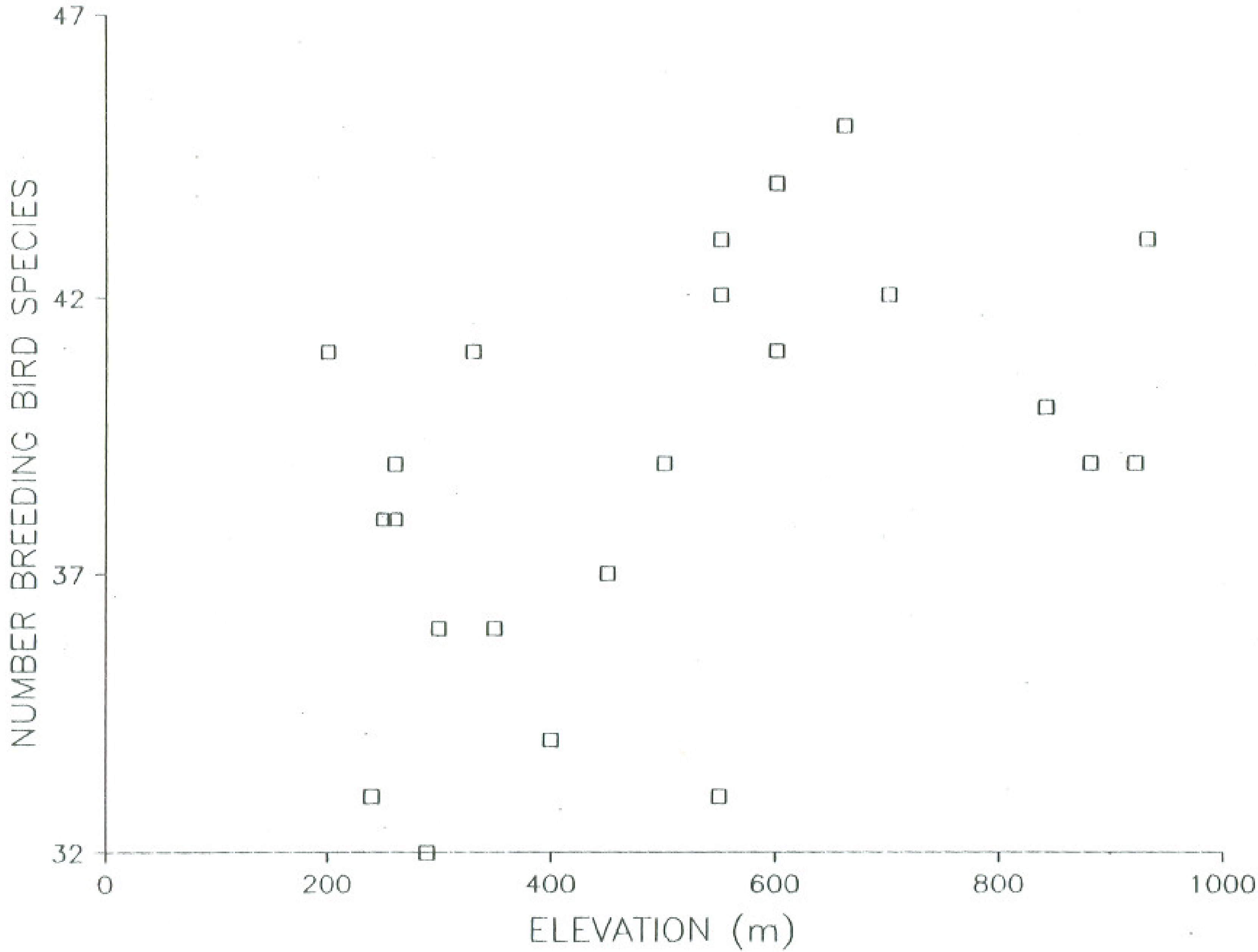
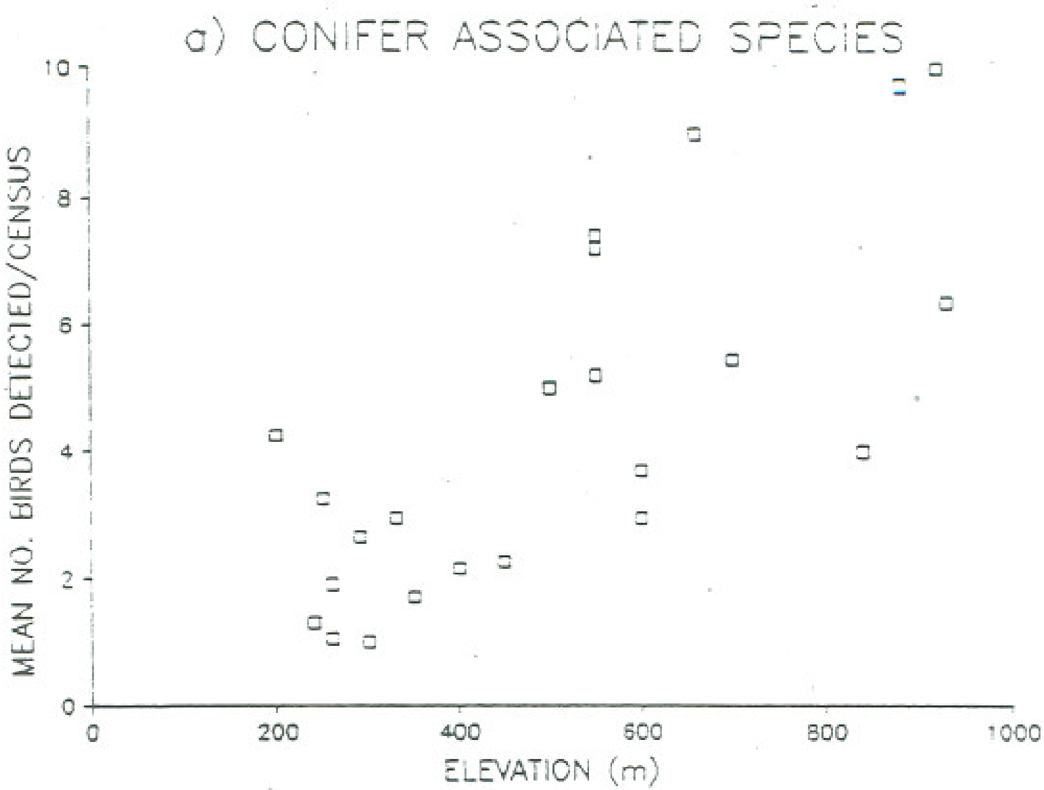


Fig. 4 Bivariate scattergram of number of breeding bird species and elevation of study plots ($R = 0.457$, $p = 0.014$).



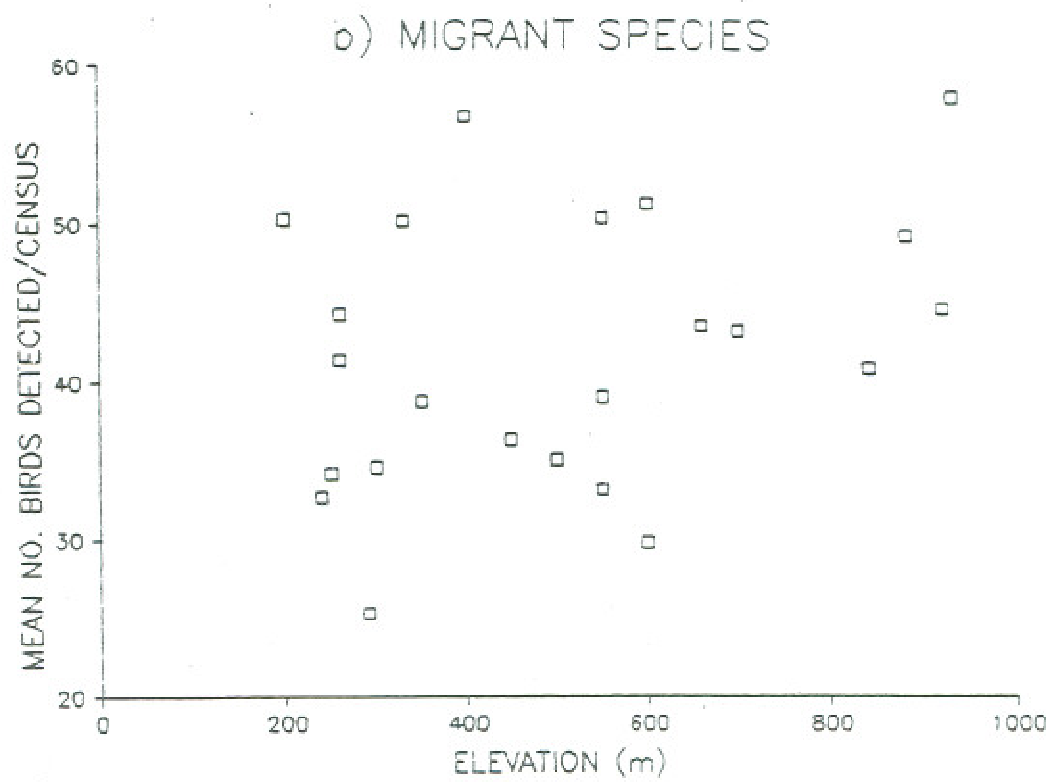


Fig. 5 Bivariate scattergrams of mean number of detections per census for two bird guilds and elevation of study plot. a) conifer-associated bird species ($R = 0.75$, $p < 0.001$). b) migrant bird species ($R = 0.616$, $p = < 0.001$).

Table 5. Principal component factor loadings for bird group abundances on 23 study plots. The eigenvalue and proportion of the variance explained by each factor are also given.

VARIABLE	FACTOR I	FACTOR II	FACTOR III
BARK FORAGERS	0.858	0.000	0.382
PRIMARY CAVITY NESTERS	0.841	0.000	0.000
SECONDARY CAVITY NESTERS	0.826	0.404	0.000
AIR SALLIERS	0.691	0.000	-0.431
GROUND FORAGERS	0.000	0.875	0.000
MIGRANTS	0.000	0.788	0.000
WINTER RESIDENTS	0.339	0.631	0.268
CONIFER-HABITAT ASSOC.	0.000	0.256	0.909
FOLIAGE FORAGERS	0.356	0.000	0.767
Eigenvalue	2.872	2.103	1.925
Percent of variation explained	31.9	23.4	21.4

Principal component 1 (PC1) accounted for 31.9 percent of the variation among plots and represented variation in the abundance of cavity nesters. Each group associated with PC1 (primary cavity nesters, secondary cavity nesters, bark foragers, and air salliers) was either dominated by or comprised entirely of cavity nesting species.

PC2 (23.4 percent) represented variation in the abundance of ground foragers, migrants, and winter residents. the postitive covariation between migrants and winter residents suggests that the populations of some resident species may have been augmented during the migration period.

PC3 (21.4 percent) represented variation in the abundance of foliage foragers and conifer associates. Most species in these two groups obtain their prey primarily from foliage. The conifer species are simply those (primarily) foliage-foragers whose distribution centers lie to the north of these oak woodlands.

Three principal components were required to explain > 75 percent of the variance. This suggests that there are at least three mostly independent sources of abundance variation in these bird communities. Groups of species represented by these principal components (Table 5) may respond to different sources of habitat and/or resource variation.

Description of Vegetation

Approximately 18,000 woody plants were mapped, identified to species, and their structure characterized in a variety of ways (see methods). Eight oak species, four other tree species, and nine shrub species occurred on the study plots (Table 6). The density of shrubs, trees, and trees and shrubs combined across species ranged from 0 to 417, 101 to 2,018, and 103 to 2,180 per 5 ha, respectively, among study plots (Fig. 6). Our plots were systematically selected to show regular and extensive variation in tree density. Although we attempted to establish all of our plots in tree stands dominated by blue oak, some plots had high densities of other deciduous oaks and tree species composition varied among all plots (Fig. 7).

Elevation varied extensively among plots (200 to 950 m) and the tree species composition of a plot was affected by its position along the elevational gradient (Fig. 8). The combined density of blue oak and buckeye had a negative relationship with elevation ($r = -0.54$, $p < 0.01$, Fig. 6a). The combined density of white oaks and bay showed a positive relationship with elevation ($r = 0.65$, $p < 0.01$, Fig. 6b).

In general, tree species diversity increased with increasing elevation (Fig. 9). This occurred primarily because of the addition of new species uncommon at lower elevations. These were tree species such as black oak, Oregon white oak, bay, and madrone whose distributional centers lie to the north of Hopland.

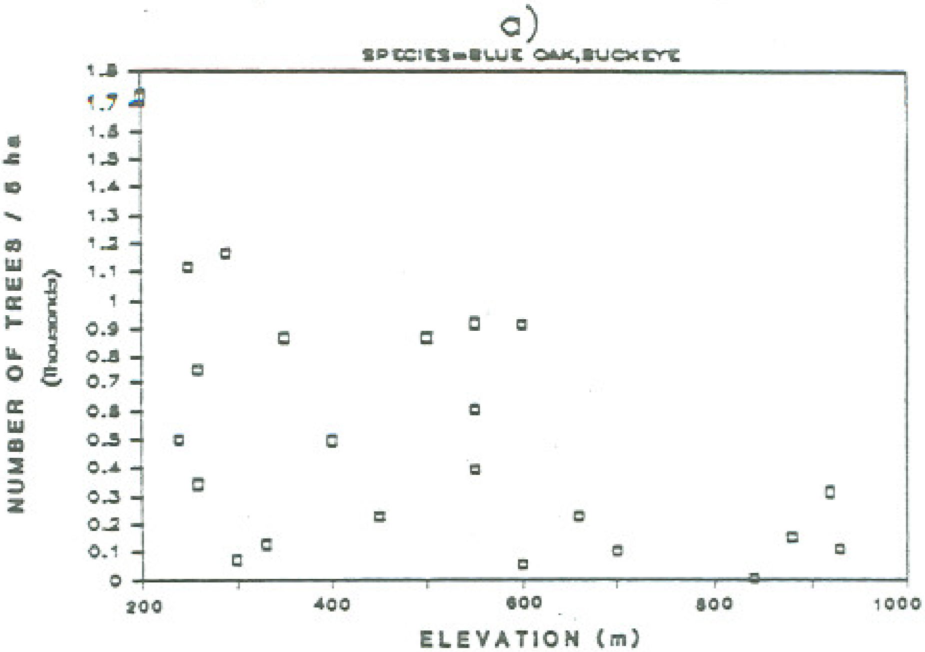
The vegetative characteristics of the plots were summarized by 32 vegetation variables (Table 7). Many of these variables were highly correlated. Total basal area per plot and the number of snags >10 cm DBH were both positively correlated with tree density ($r = 0.69$ and $r = 0.63$, Fig. 10a and 10c, respectively). Number of shrubs was also positively correlated with tree density ($r = 0.71$. $p < 0.01$, Fig. 6). In contrast, mean basal area per tree was negatively correlated with tree density ($r = -0.76$, $p < 0.01$, Fig. 10b). These relationships

Table 6. Tree and shrub species detected based on data from all study plots. Mnemonic for species group, common and scientific names of species in group, percent frequency of occurrence (% FREQ) across all study plots, mean number of stems per plot (x), and range in number of stems are listed.

MNEMONIC	COMMON NAME	SCIENTIFIC NAME	% FREQ	x STEMS/5ha	RANGE
<u>OAK TREE SPECIES</u>					
BLUE	Blue Oak	<u>Quercus douglassii</u>	100	467.1	5 - 1643
LIVE	Interior live oak Coast live oak Canyon live oak	<u>Quercus wislizenii</u> <u>Quercus agrifolia</u> <u>Quercus chrysolepis</u>	100	63.4	12 - 182
WHITE	Valley oak Oregon white oak	<u>Quercus lobata</u> <u>Quercus garryana</u>	91	58.3	0 - 423
BLACK	Black oak	<u>Quercus kellogii</u>	78	26.9	0 - 143
ORACLE	Oracle oak	<u>Quercus morehus</u>	70	2.8	0 - 20
<u>OTHER TREE SPECIES</u>					
BUCK	Buckeye	<u>Aesculus californica</u>	83	56.9	0 - 350
BAY	Califonia bay	<u>Umbellularia californica</u>	70	14.0	0 - 86
MAD	Madrone	<u>Arbutus menzesii</u>	48	5.1	0 - 52
ASH	Oregon ash	<u>Fraxinus latifolia</u>	4	0.2	0 - 5

Table 6 cont.

COMMON NAME	SCIENTIFIC NAME	FREQ	X	RANGE
SHRUBS				
Poison oak	Toxicodendron diversilobum	96	5.1	0 - 18
Coffeeberry	Rhamnus californica	52	8.5	0 - 61
Scrub oak	Quercus dumosa	48	3.6	0 - 22
Mountain mahogony	Cercocarpus betuloides	39	3.3	0 - 44
Gooseberry	Ribes sp.	22	0.5	0 - 3
Elderberry	Sambucus caerulea	17	1.0	0 - 11
Chamise	Adenostoma fasciculatum	9	1.5	0 - 29
Wild grape	Vitus californica	9	0.4	0 - 8
Honeysuckle	Lonicera sp.	4	<0.1	0 - 1



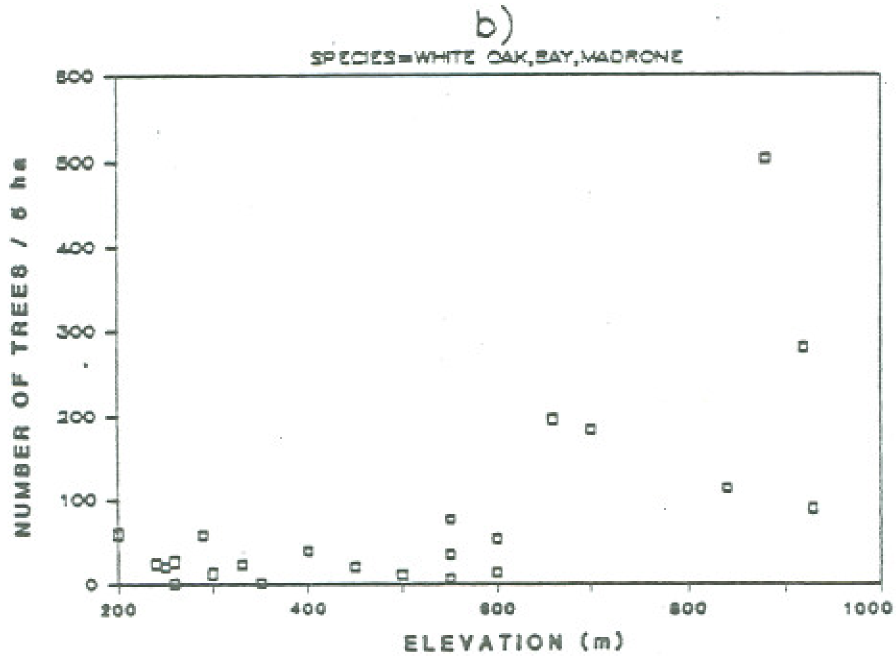


Figure 8. Bivariate scattergrams of tree species composition and elevation of study plots. a) the number of blue oak and buckeye versus elevation. b) the number of white oak, bay, and madrone versus elevation.

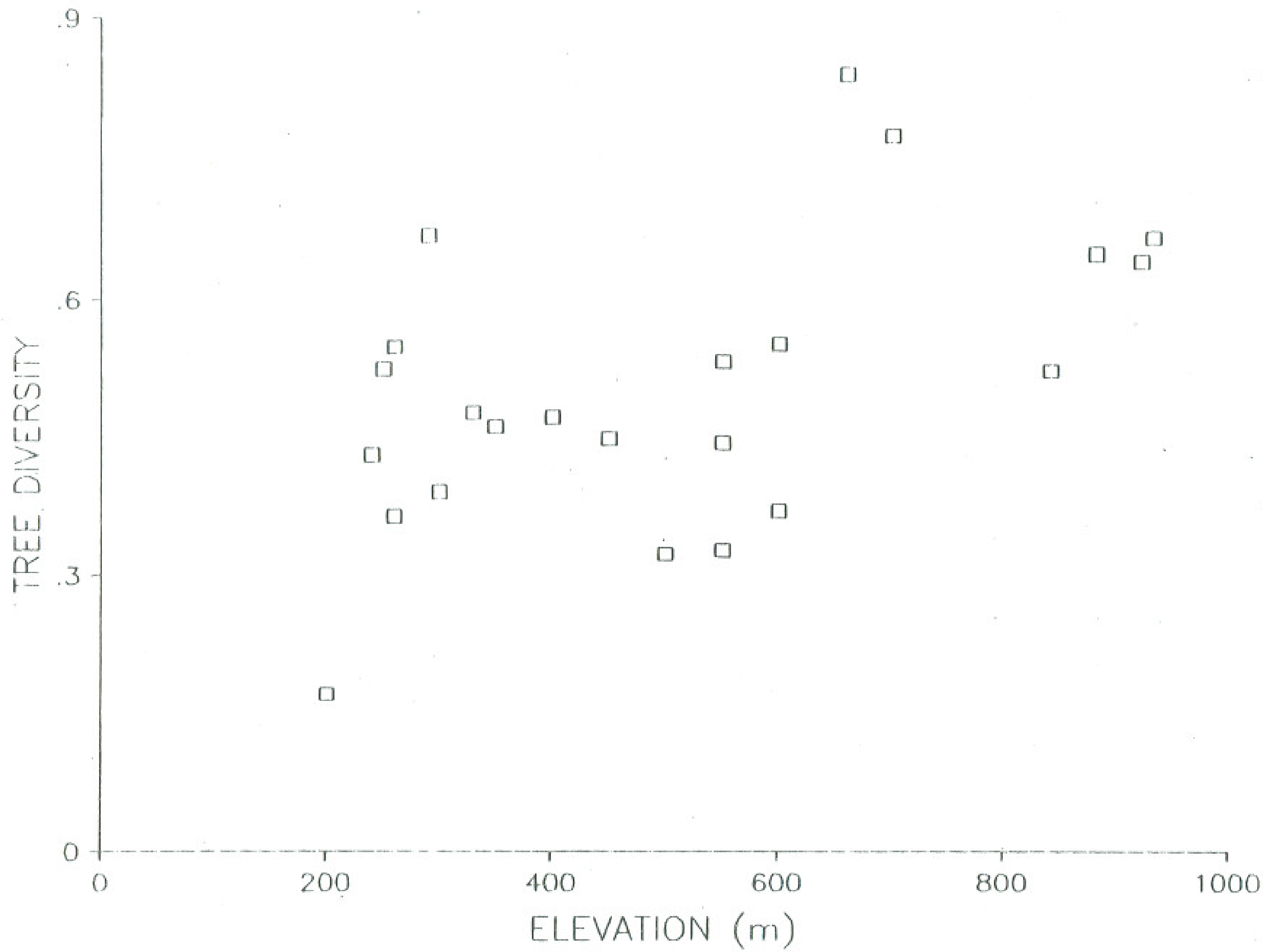


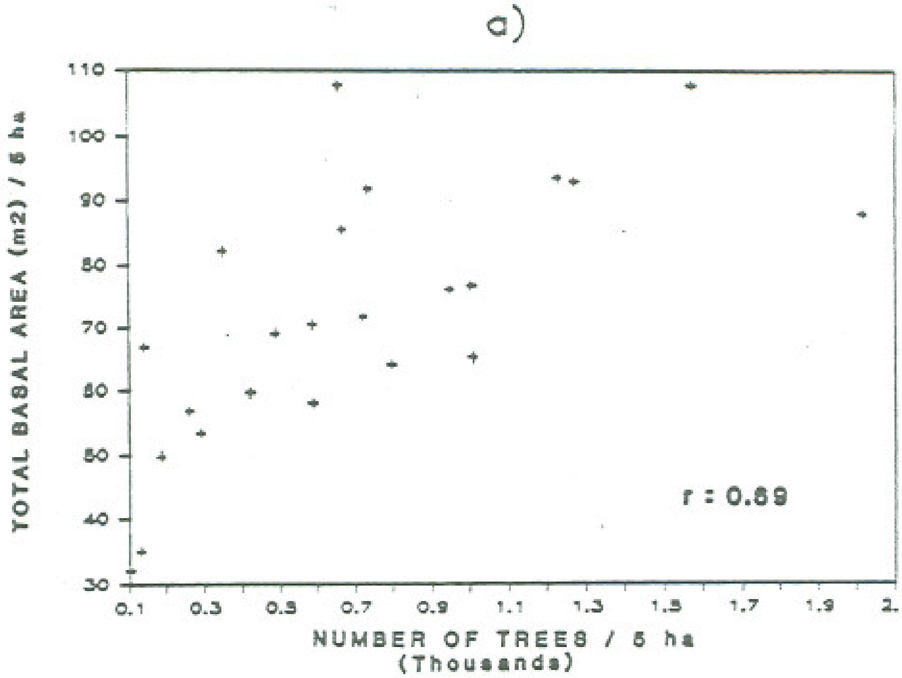
Fig. 9 Bivariate scattergram of tree diversity index (Shannon-Weaver) and elevation of 23 study plots ($R = 0.457$, $p = 0.014$). Tree diversity index ranges from 0 (low diversity) to 1.0 (high diversity).

Table 7. Variables describing vegetation floristics and structure of the study plots. Variables used in principal components analysis of the vegetative community are identified.

MNEMONIC	USED IN PCA	VARIABLE	DERIVATION
FLORISTICS:			
BLUE1	X	Number of blue oaks >5-10cm DBH.	Direct count.
BLUE2	X	Number of blue oaks >10-25cm DBH.	Direct count.
BLUE3	X	Number of blue oaks >25-50cm DBH.	Direct count.
BLUE4	X	Number of blue oaks >50cm DBH.	Direct count.
BLUE		Total number of blue oaks.	Direct count.
WHITE1	X	Number of white oaks >5-25cm DBH.	Direct count.
WHITE2	X	Number of white oaks >25-50cm DBH.	Direct count.
WHITE3	X	Number of white oaks >50cm DBH.	Direct count.
WHITE		Total number of white oaks.	Direct count.
LIVE1	X	Number of live oaks >5-25cm DBH.	Direct count.
LIVE2	X	Number of live oaks >25-50cm DBH.	Direct count.
LIVE3	X	Number of live oaks >50cm DBH.	Direct count.
LIVE		Total number of live oaks.	Direct count.
BALIVE	X	Basal area (m2) of live oaks.	Sum of basal area of each stem of a tree (DBH*DBH*.007854) summed over all trees.
BLACK1	X	Number of black oaks >5-25cm DBH.	Direct count.
BLACK2	X	Number of black oaks >25-50cm DBH.	Direct count.
BLACK3	X	Number of black oaks >50cm DBH.	Direct count.
BLACK		Total number of black oaks.	Direct count.
BUCK	X	Total number of buckeye.	Direct count.
BABUCK	X	Basal area (m2) of buckeye.	Sum of basal area of all trees.
BAY	X	Total number of bay trees.	Direct count.
BABAY	X	Basal area (m2) of bay trees.	Sum of basal area of all trees.
MAD	X	Total number of madrone.	Direct count.
BAMAD	X	Basal area (m2) of madrone.	Sum of basal area of all trees.
SHRUB	X	Total number of shrubs and vines.	Direct count.
TREDIV		Tree species diversity index.	Shannon index.

Table 7. cont.

MNEMONIC	USED IN PCA	VARIABLE	DERIVATION
STRUCTURE:			
TOTLTRE		Total number of trees.	Direct count.
TOTLBA	X	Total basal area of all trees.	Sum of basal area of all trees.
AVEBA	X	Average basal area (m2) per tree.	Total basal area divided by total number of trees.
CC	X	Percent canopy closure.	Dot count on aerial photo (1:7000).
DEC		Number of dead trees >10cm DBH.	Direct count.
CAV		Cavity density index.	Sum of weighted rank values for natural and excavated cavities in each tree (rank1*1, rank2*2) summed over all trees.



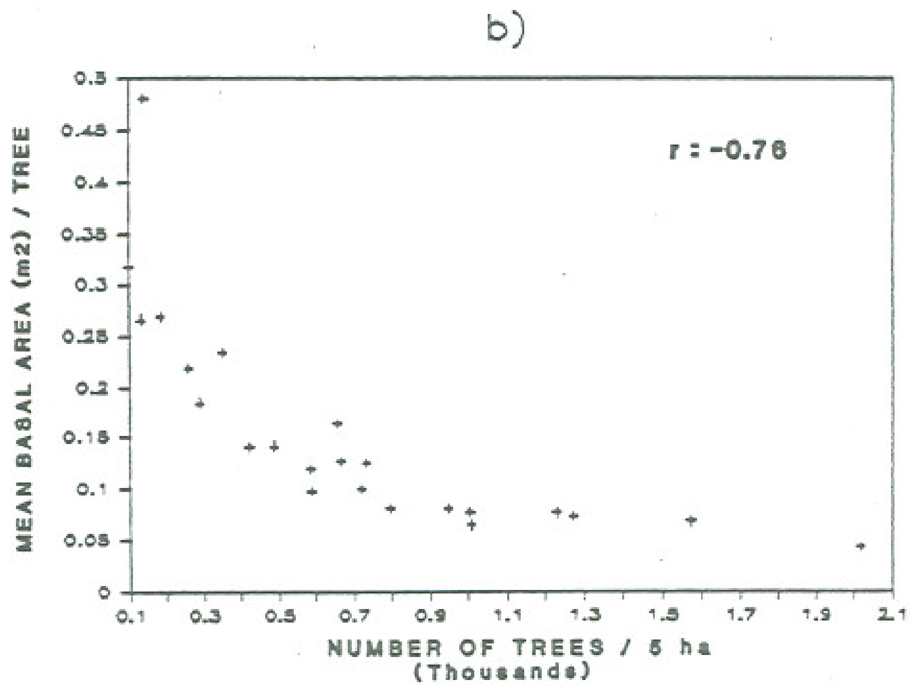


Figure 10. Bivariate scattergrams of three structural characteristics versus tree density on the 23 study plots. a) total basal area versus tree density. b) mean basal area per tree versus tree density. c) number of snags >10 cm DBH versus tree density.

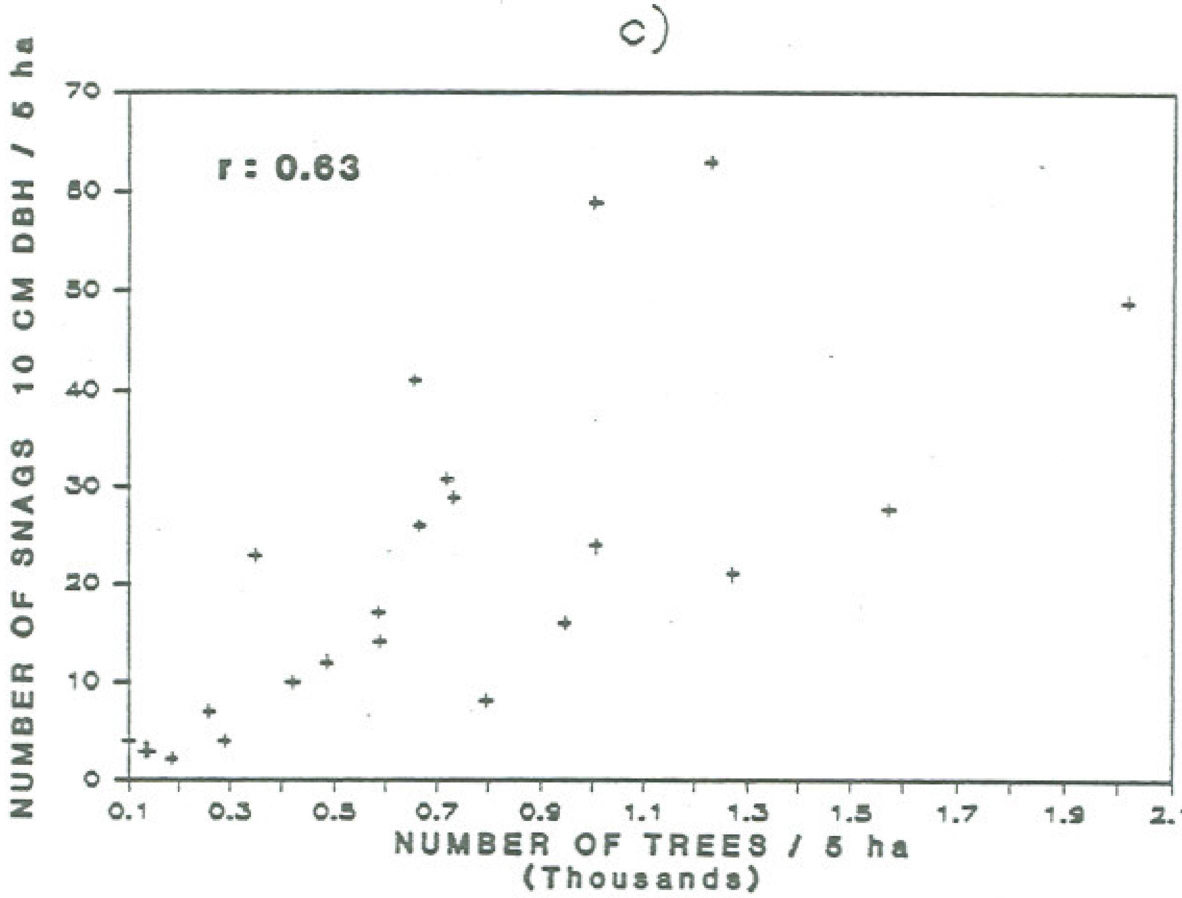


Figure 10 cont.

reveal that denser stands of trees typically have smaller diameter trees, a denser understory of shrubs, and a greater number of snags >10 cm DBH.

Multivariate Analysis of the Vegetation

Principal components were estimated from the correlation matrix (Appendix A) of the 22 untransformed vegetation variables described by their mean values and counts for each plot. Variables used in the analysis represented both structural and compositional aspects of each study plot (Table 7). Six principal components with eigenvalues >1.0 described 88.6 percent of the variation in vegetation structure and composition among plots (Table 8).

Principal component 1 (PC1) accounted for 21.1 percent of the variation among plots and represented a tree density continuum. PC1 simply reflected the design of our study; that is to systematically sample a range of study plots varying extensively in their tree densities.

PC2 (19.9 percent) represented variation in the number and basal area of live oaks and madrone, the most abundant evergreen species. In addition, the large average size of most live oaks and madrones caused their densities to greatly influence the total basal area of a plot.

PC3 (14.1 percent) represented a blue oak to white oak and bay vegetation gradient related to elevation (Fig. 8). Large blue oaks (>50 cm DBH) occurring on lower elevation plots were gradually

Table 8. Principal component factor loadings for vegetative characteristics of study plots. The eigenvalue and proportion of the variance explained by each factor are given.

VARIABLE	FACTOR I	FACTOR II	FACTOR III	FACTOR IV	FACTOR V	FACTOR VI
LIVE1	0.891	0.000	0.000	0.000	0.000	0.000
BLACK1	0.826	0.000	0.000	0.000	0.310	0.356
BLUE2	0.802	0.000	0.000	0.450	0.000	0.000
BLUE1	0.799	0.000	0.000	0.000	0.000	0.000
SHRUBS	0.717	0.000	0.000	0.000	0.000	0.000
CC	0.639	0.360	0.000	0.579	0.000	0.000
BALIVE	0.000	0.942	0.000	0.000	0.000	0.000
LIVE3	0.000	0.895	0.000	-0.316	0.000	0.000
LIVE2	0.328	0.834	0.000	0.000	0.000	0.000
MADRONE	0.000	0.832	0.000	0.000	0.000	0.412
BAMAD	0.000	0.788	0.000	0.000	0.000	0.537
TOTALBA	0.375	0.599	0.382	0.425	0.000	0.000
WHITE1+2	0.000	0.000	0.884	0.000	0.000	0.000
WHITE3	-0.262	0.000	0.855	-0.341	0.000	0.000
BAY	0.000	0.317	0.814	0.000	0.000	0.000
BLUE4	0.000	0.000	-0.700	0.454	0.337	0.000
AVEBA	-0.396	0.000	0.000	-0.815	0.000	0.000
BLUE3	0.457	0.000	-0.355	0.719	0.000	0.000
BUCKEYE	0.000	0.000	0.000	0.000	0.928	0.000
BABUCK	0.000	0.000	0.000	0.000	0.921	0.000
BLACK3	0.000	0.000	0.000	0.000	0.000	0.946
BLACK2	0.388	0.000	0.000	0.000	0.356	0.800
Eigenvalue	4.660	4.377	3.097	2.652	2.377	2.340
Proportion of variation explained	21.1	19.9	14.1	12.1	10.8	10.6

replaced by white oaks of varying sizes on higher elevation plots. Bay trees occurred in ravines at mid to high elevations.

PC4 (12.1 percent) represented the negative relationship between the density of mid-sized blue oaks (>25-50 cm DBH) and the average size of trees on our study plots. PC4 is another factor resulting from the sampling design of our study; the size of blue oaks (and most other tree species occurring on a plot) was negatively related to tree density.

PC5 (10.8 percent) represented the abundance of buckeye trees. Buckeye trees were most abundant in moist ravines and ungrazed areas. PC6 (10.6 percent) represented variation in the abundance of black oaks, which became more common at higher elevations.

Bird/Habitat Relationships

Tree use by cavity nesting birds. -- Of the approximately 16,000 trees we measured, 2,207 contained natural cavities and 412 had excavated cavities, a ratio of 6:1. Tests of the equality of used and available tree species distributions were rejected for both minor ($X^2 = 815$, df = 4, $p < 0.001$) and major ($X^2 = 180$, df = 4, $p < 0.001$) natural cavity tree species. Trees with 1-3 natural cavities occurred in evergreens (21 percent) and buckeye (21 percent) in greater proportion than their availability (11 and 8 percent,respectively; Fig. 11, Appendix B). For trees species with greater than three natural cavities, cavities occurred in evergreens (predominantly live oaks) in significantly greater numbers than expected (Fig. 11,

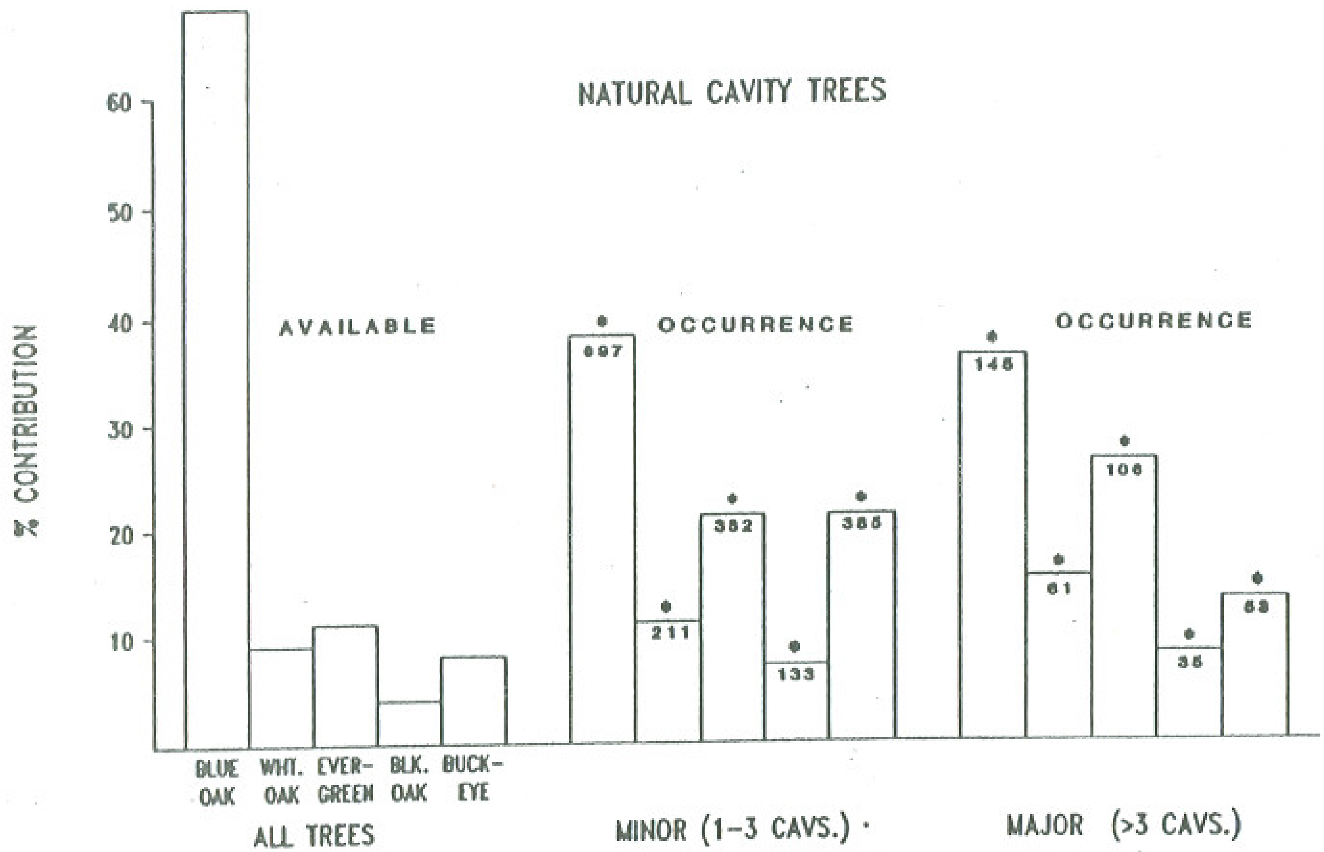


Figure 11. Natural cavity occurrence by tree species compared with tree species availability. Two catagories of abundance, minor and major, indicate trees with 1-3 cavities and > 3 cavities, respectively. Sample size for each tree species by cavity group is listed. * indicate a significant ($p < 0.05$) deviation from expected.

Appendix B). The majority of natural cavities occurred in blue oaks, though less than predicted by their availability.

Tests of the equality of used and available tree species distributions were rejected for both minor (X^2 = 181, df = 4, $p <$ 0.001) and major excavated cavity tree species (X^2 = 102, df = 4, $p <$ 0.001, respectively; Fig. 12). For trees with excavated cavities, white oaks were chosen disproportionately to their availability (Fig. 12). White oaks made up nine percent of those trees we measured, yet comprised 30 and 36 percent of the trees containing 1-3 and >3 cavities, respectively (Appendix B). Though a small percentage of the total, black oaks also contained more excavated cavities than expected ($p < 0.05$). The majority of excavated cavities occurred in blue oaks, though in numbers not different from that predicted by their availability.

As expected, the average size of the trees differed between groups with different numbers of natural and excavated cavities (Figs. 13 and 14, respectively). The number of natural cavities occurring in trees increased with DBH (Fig. 13). When all trees are combined, the increase is highly significant (F = 632, df = 2, $p < 0.001$). This pattern holds true for individual tree species, as well as all tree species combined. In general, the number of excavated cavities occurring in trees also increased with DBH (F = 384, df = 3, $p <$ 0.001, Fig. 14). The only exceptions were for evergreen oaks and buckeye (Fig. 14). Starts indicate cavity excavations abandoned before completion. The DBH of trees with excavated cavity starts were intermediate to those without any excavated cavities and those with from 1-3 cavities. This suggests that there may be a critical minimum

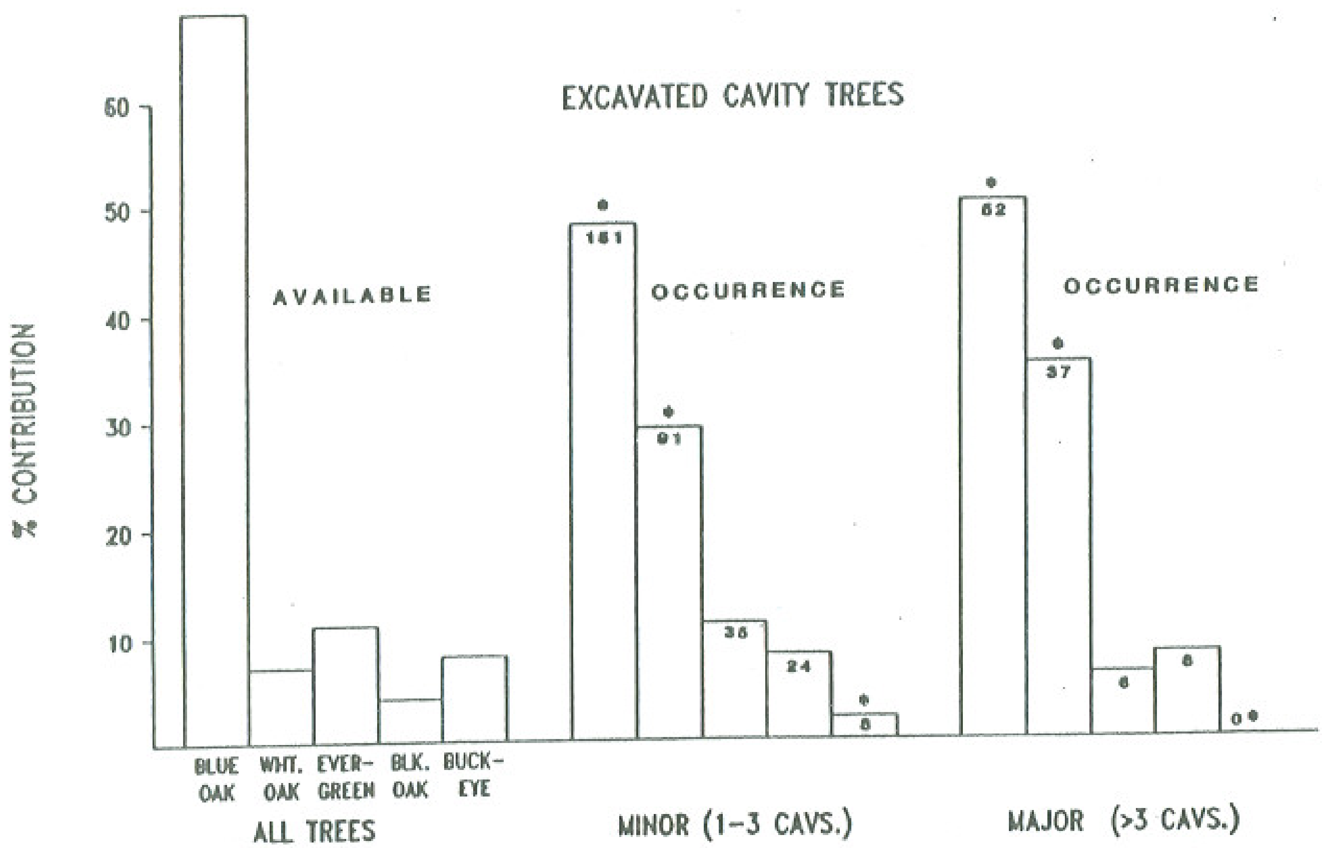


Figure 12. Excavated cavity occurrence by tree species compared with tree species availability. Two catagories of abundance, minor and major, indicate trees with 1-3 cavities and > 3 cavities, respectively. Sample size for each tree species by cavity group is listed. * indicate a significant ($p < 0.05$) deviation from expected.

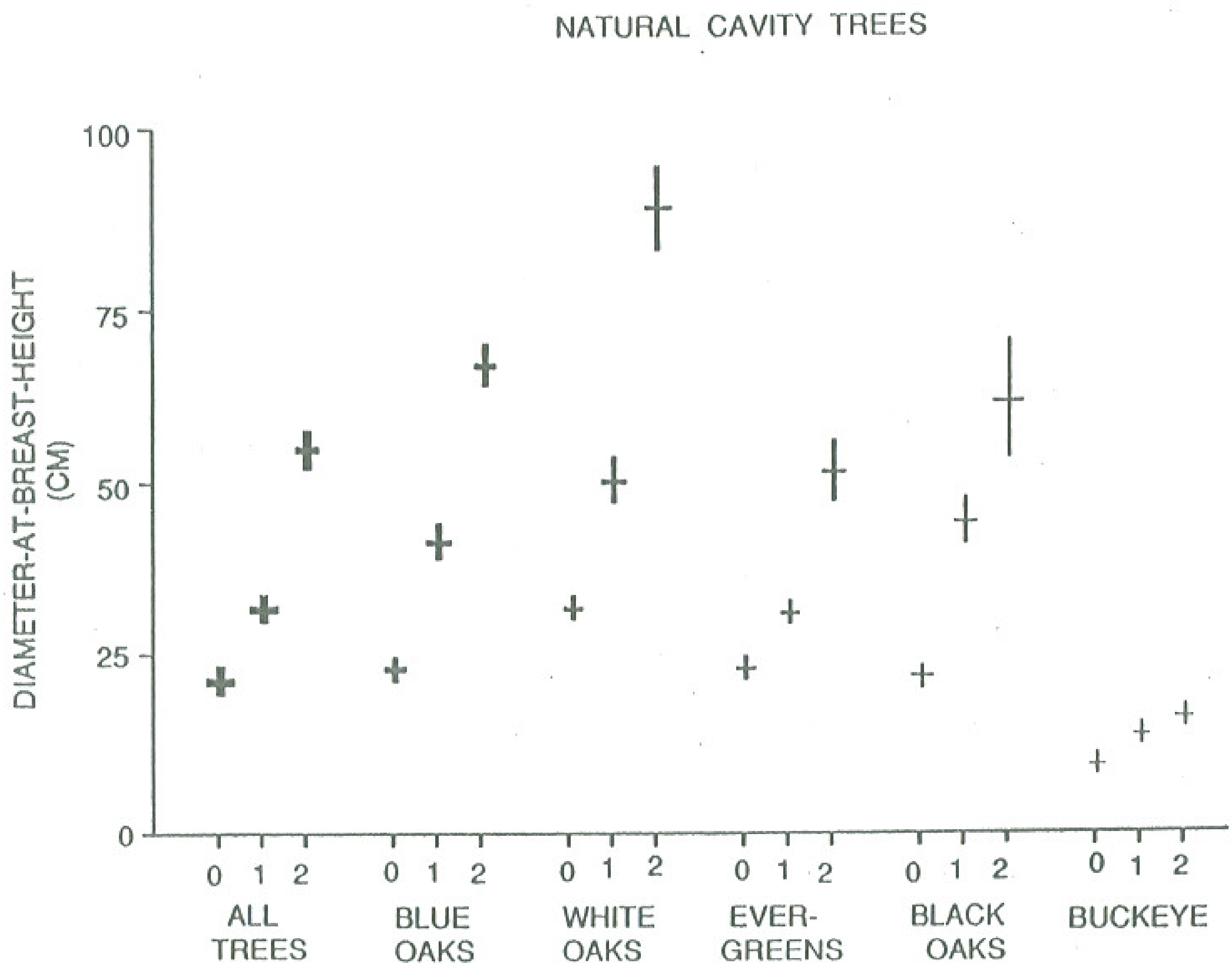


Figure 13. Mean tree diameter by species for natural cavity abundance. 0 = trees without natural cavities. 1 = trees with 1-3 cavities. 2 = trees with >3 cavities. Vertical bars indicate 95% confidence intervals.

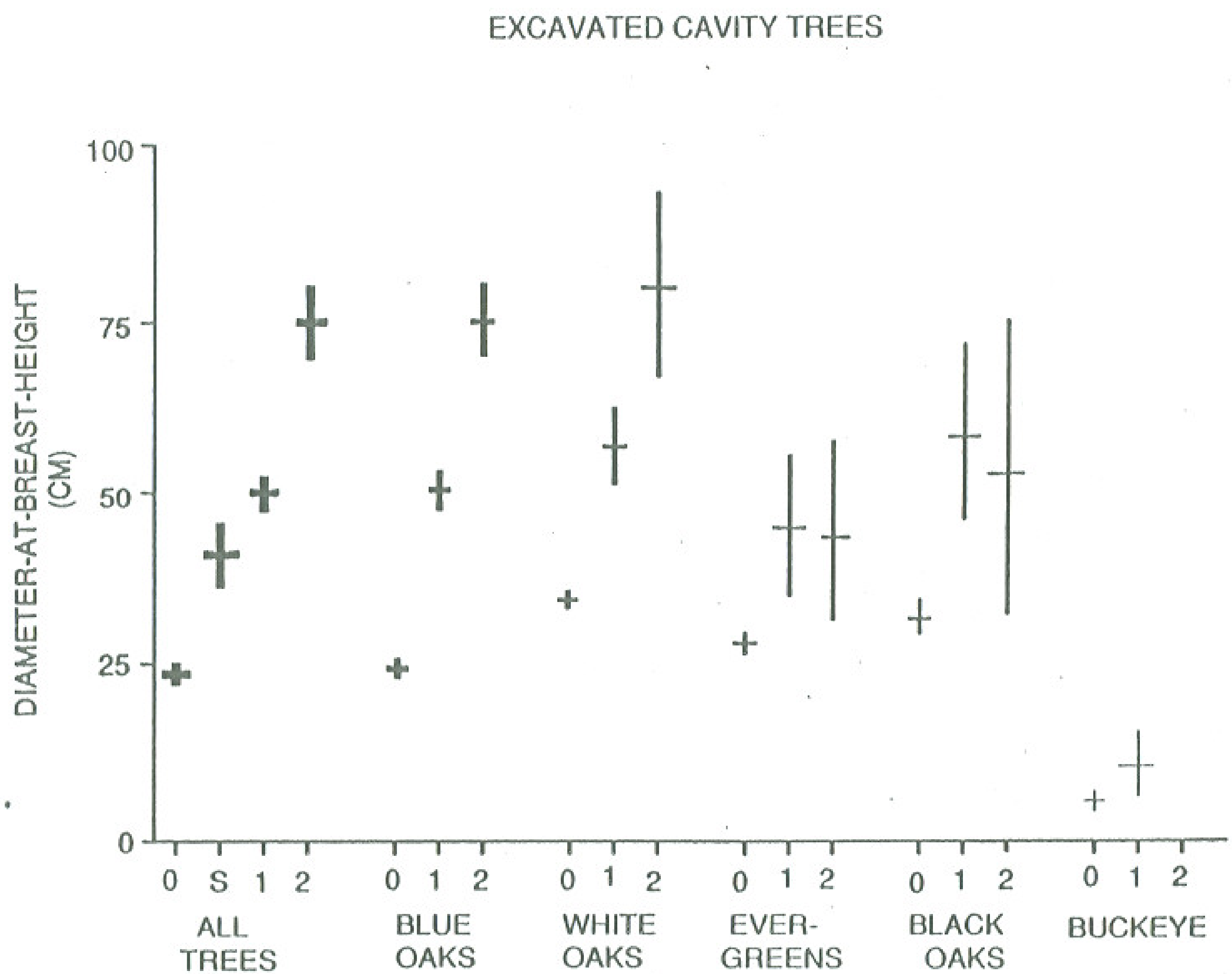


Figure 14. Mean tree diameter by species for excavated cavity abundance. 0 = trees without excavated cavities. 1 = trees with 1-3 cavities. 2 = trees with >3 cavities. 3 = trees with cavity starts (i.e. incomplete). Vertical bars indicate 95% confidence intervals.

limb diameter needed for the successful completion of cavity excavation by woodpeckers.

Granaries. -- Acorn storage trees were categorized into two groups: (1) minor, less than 10 percent of the tree used for storage; and (2) major, >10 percent of the tree used for storage. Test of the equality of used and available acorn storage tree species distributions were rejected for both minor ($X^2 = 90$, df = 4, $p < 0.001$) and major cavities ($X^2 = 62$, df = 4, $p < 0.001$, Fig. 15). White oaks (*Q. lobata*) were chosen in greater numbers than expected based on their availability. White oaks comprised 9.5 percent of all trees, and yet make up 25 percent of minor storage trees and close to 50 percent of major storage trees (Fig. 15, Appendix C).

There was a general trend for a species' use as a granary tree to increase as the diameter of the tree increased (Fig. 16). When all trees were combined, the increase was significant ($F = 189$, df = 2, $p < 0.001$). However, the pattern was more variable when tree species were looked at individually. Blue oaks and black oaks granaries were larger than non-granary trees, but there was no difference between minor and major use (Fig. 16). In contrast, granary use increased in white oaks as their diameters increased.

Nest and tree selection by cavity nesting birds. -- Three hundred and sixty nests of cavity nesting species were found during the breeding season of 1986 and 1987 (Table 1). We compared relative use of excavated versus natural cavities for nest sites for those bird species (n = 7) with sufficient data (Fig. 17). These species were

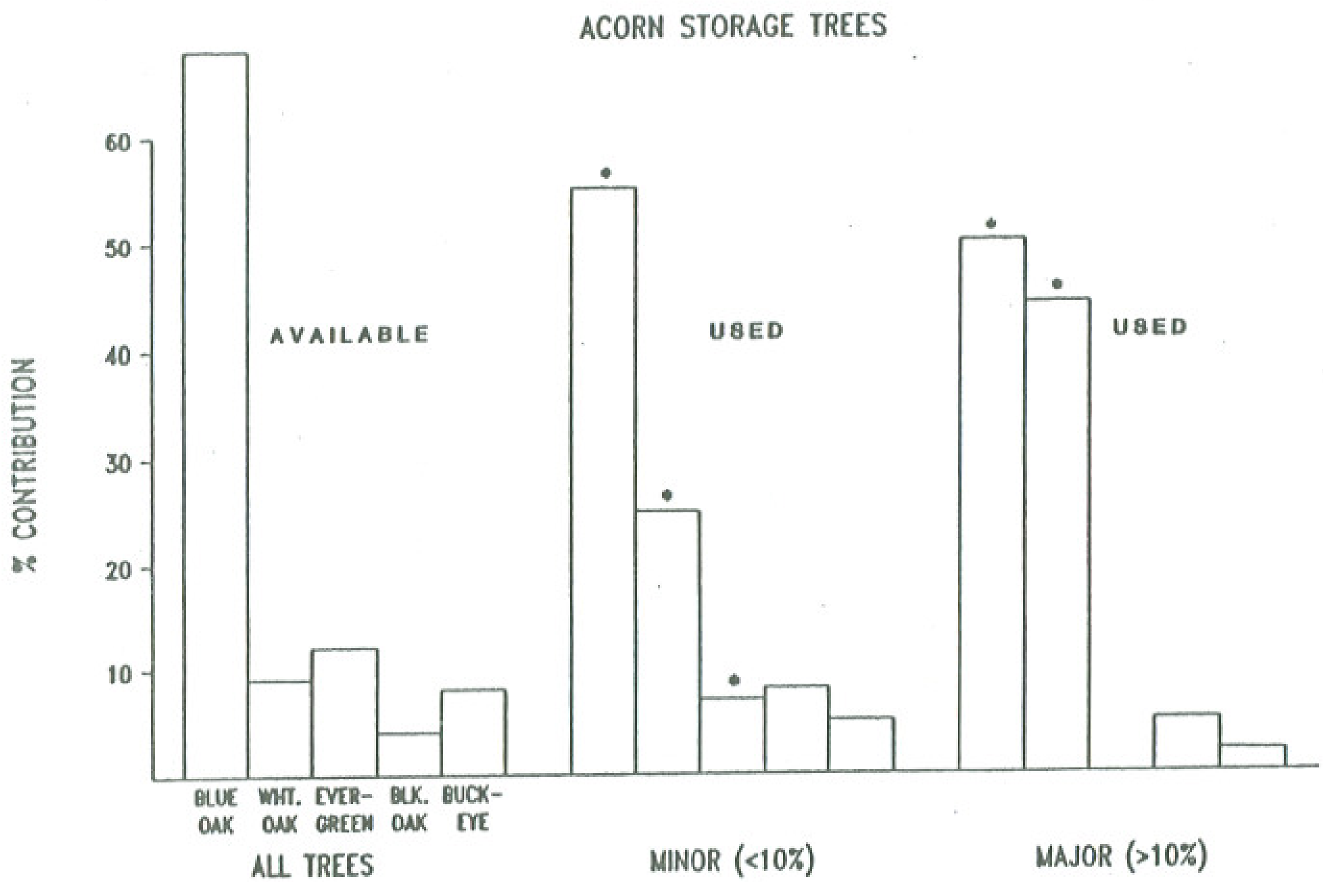


Figure 15. Tree species used for granaries compared to tree species availability. Two use catagories, minor and major, were used to describe <10% and >10% use, respectively, of the tree bark surface for storage of acorns. * indicate a significant ($p < 0.05$) deviation from expected.

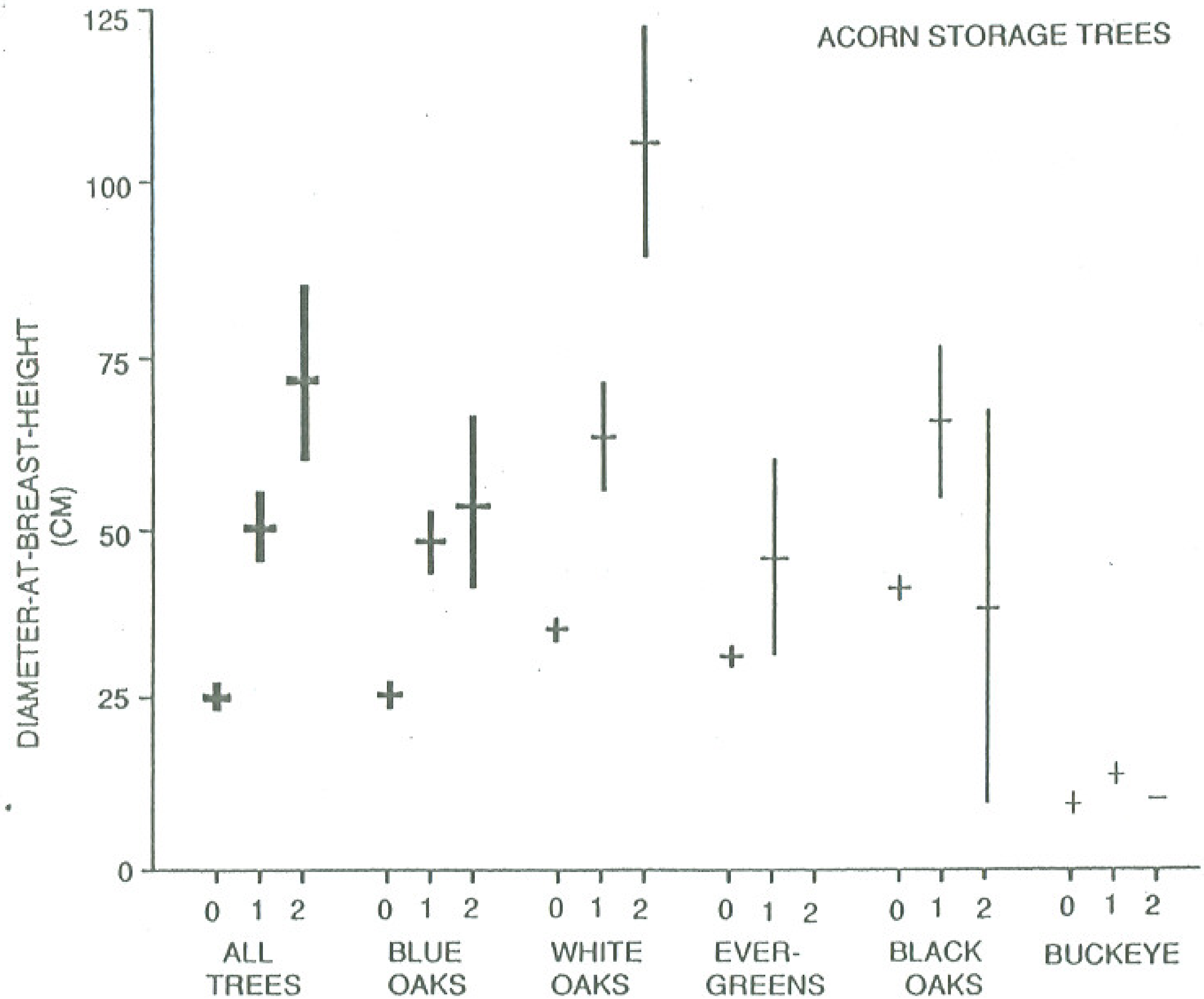


Figure 16. Mean tree diameter by species for acorn storage tree use. 0 = trees not used for acorn storage. 1 = trees with <10% of bark surface containing acorns. 2 = trees with >10% of bark surface containing acorns. Vertical bars indicate 95% confidence intervals.

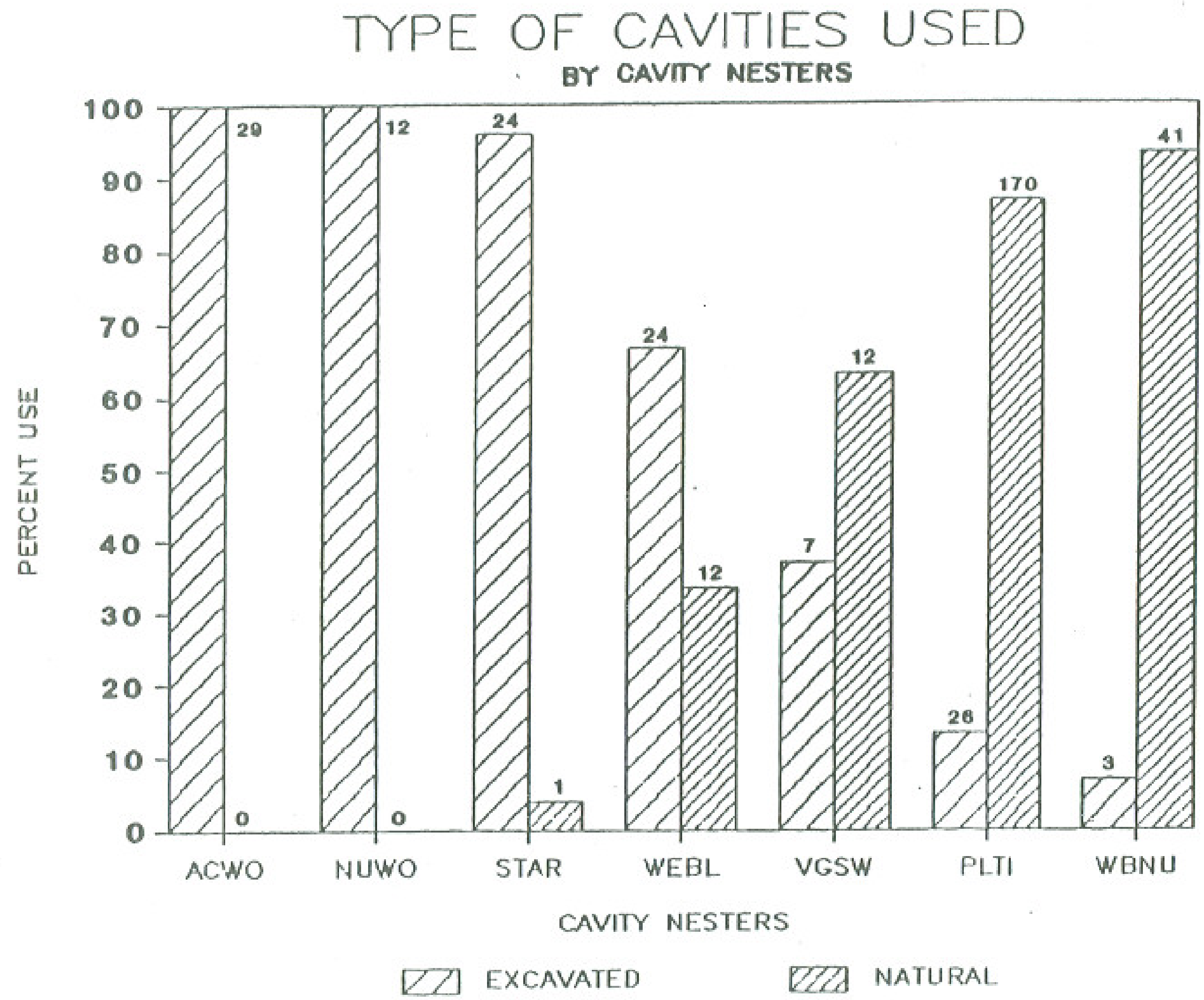


Figure 17. Proportions of cavity type used for nesting by seven bird species at Hopland, California. Number of nests found during 1986 and 1987 are listed.

arranged from those exclusively using excavated cavities (Acorn woodpecker and Nuttall's woodpecker) to predominantly natural cavity nesters (Plain titmouse and White-breasted nuthatch). Of the seven, only the Western bluebirds and Violet-green swallows chose both natural and excavated cavities in approximately equal numbers (Fig. 17). European starlings were found 95 percent of the time in excavated cavities. In addition to a trend of separation by cavity type, these species chose tree species in varying proportions for both natural and excavated cavities (Figs. 18 and 19, respectively). For Plain titmouse in natural cavities, black oaks were chosen in greater numbers than predicted, whereas buckeye was chosen less (Appendix D). For nests in excavated cavities, Plain titmouse chose trees in proportion to their availability ($X^2 = 6.5$, df = 4, $p > 0.10$). White-breasted nuthatches also chose tree species with natural cavities in proportion to availability ($X^2 = 15.36$, df = 4, $p > 0.05$). These two species are potential competitors for cavities, since both preferred natural cavities, chose similar tree species, and were both early nesters (late March). P. Manley witnessed a White-breasted nuthatch displacing a Plain titmouse from a natural cavity on one of our plots.

Preliminary analysis of nest tree information indicated that White-breasted nuthatches chose cavities significantly lower in the trees than did Plain titmouse ($t = 2.38$, df =73, $p = 0.02$; Mayville unpublished, Humboldt State University, Arcata,CA). Plain titmouse chose nest cavities at an average height of 5.9 m, whereas White-breasted nuthatches chose cavities averaging 4.3 m. Another interesting finding was that White-breasted nuthatches were using

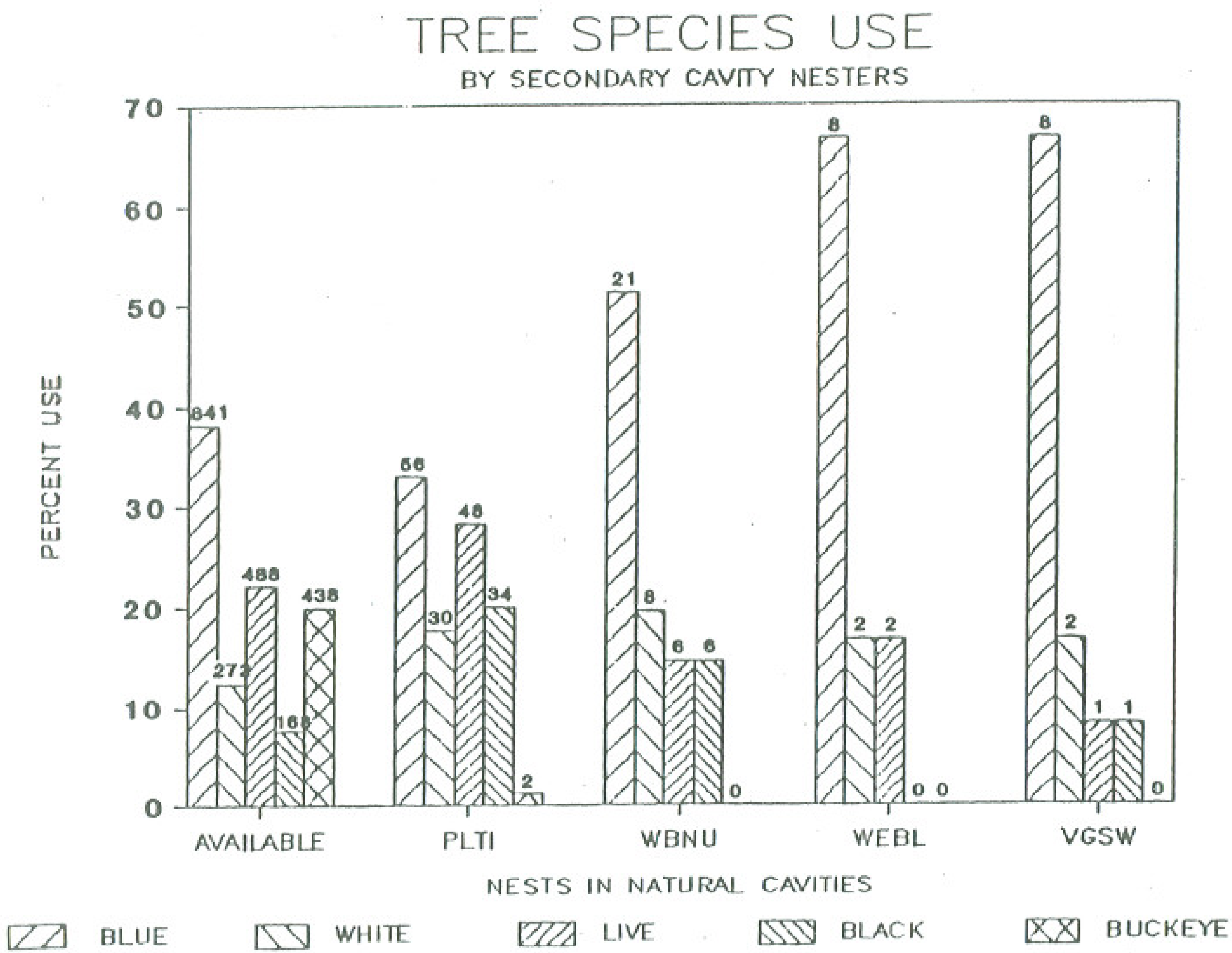


Figure 18. Nest tree selection by secondary cavity nesters in natural cavities compared to natural cavity availability by tree species. Sample size is indicated above bars.

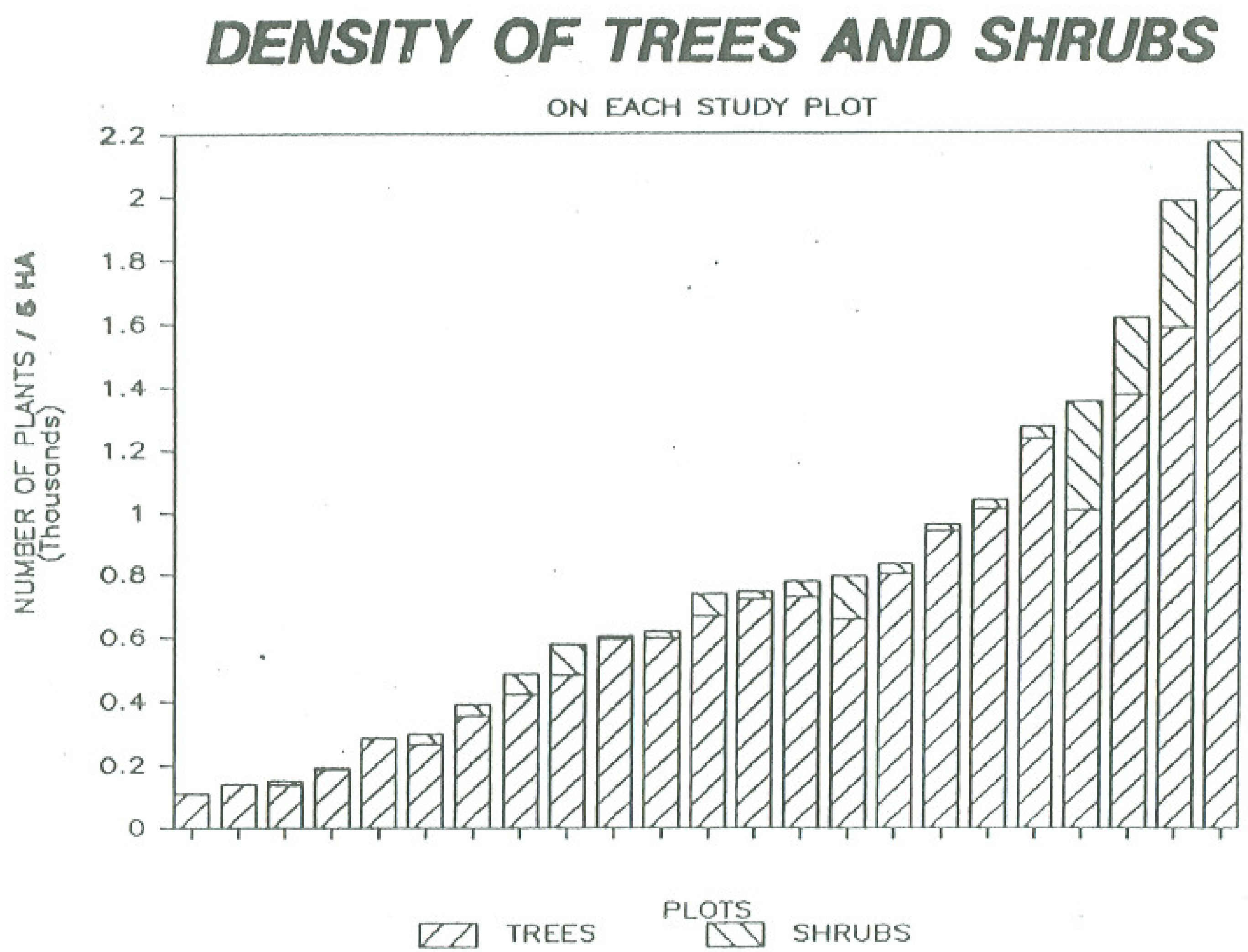


Figure 6. Total number of trees and shrubs on each of the 23 study plots.

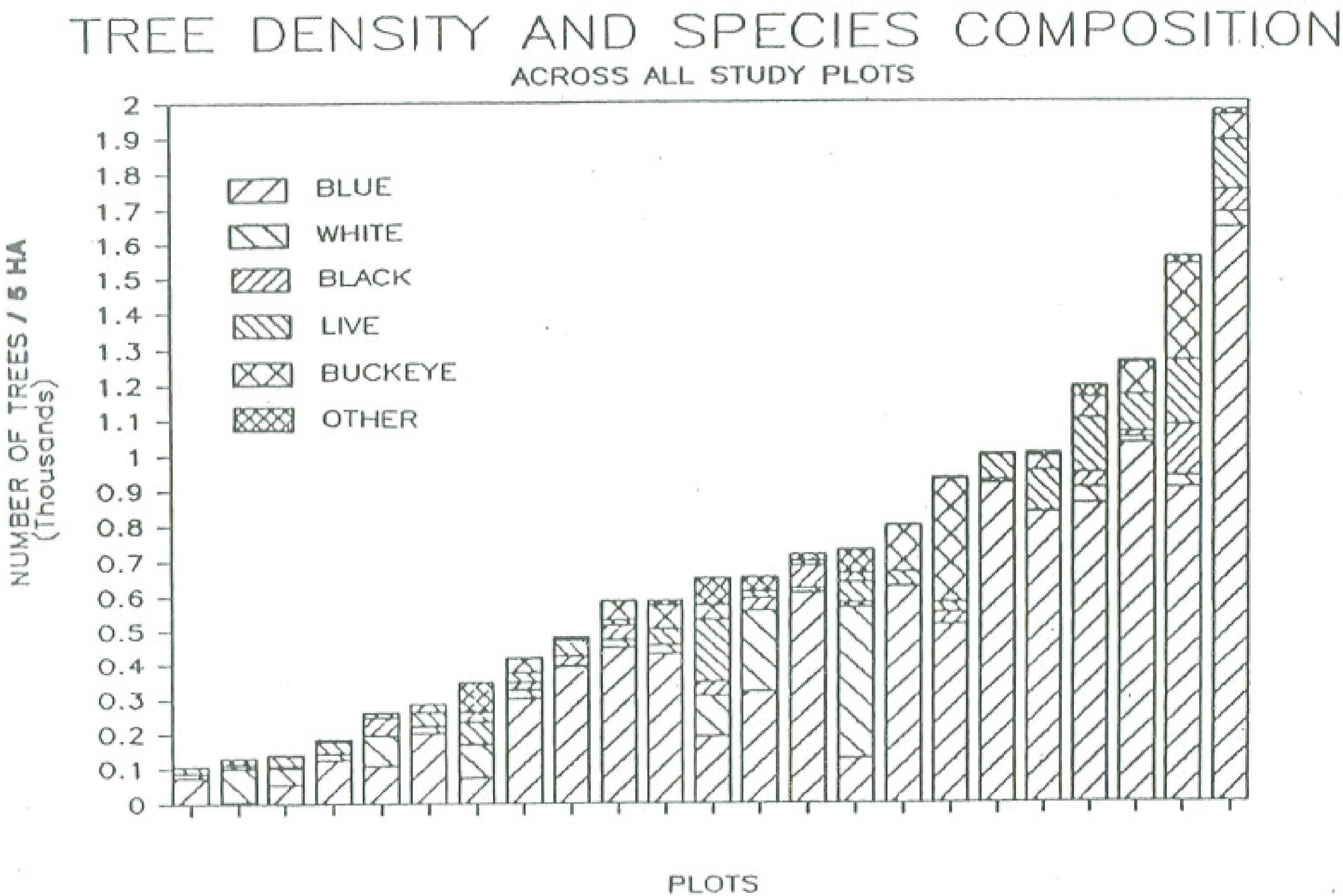


Figure 7. Tree density and species composition on each of the 23 study plots.

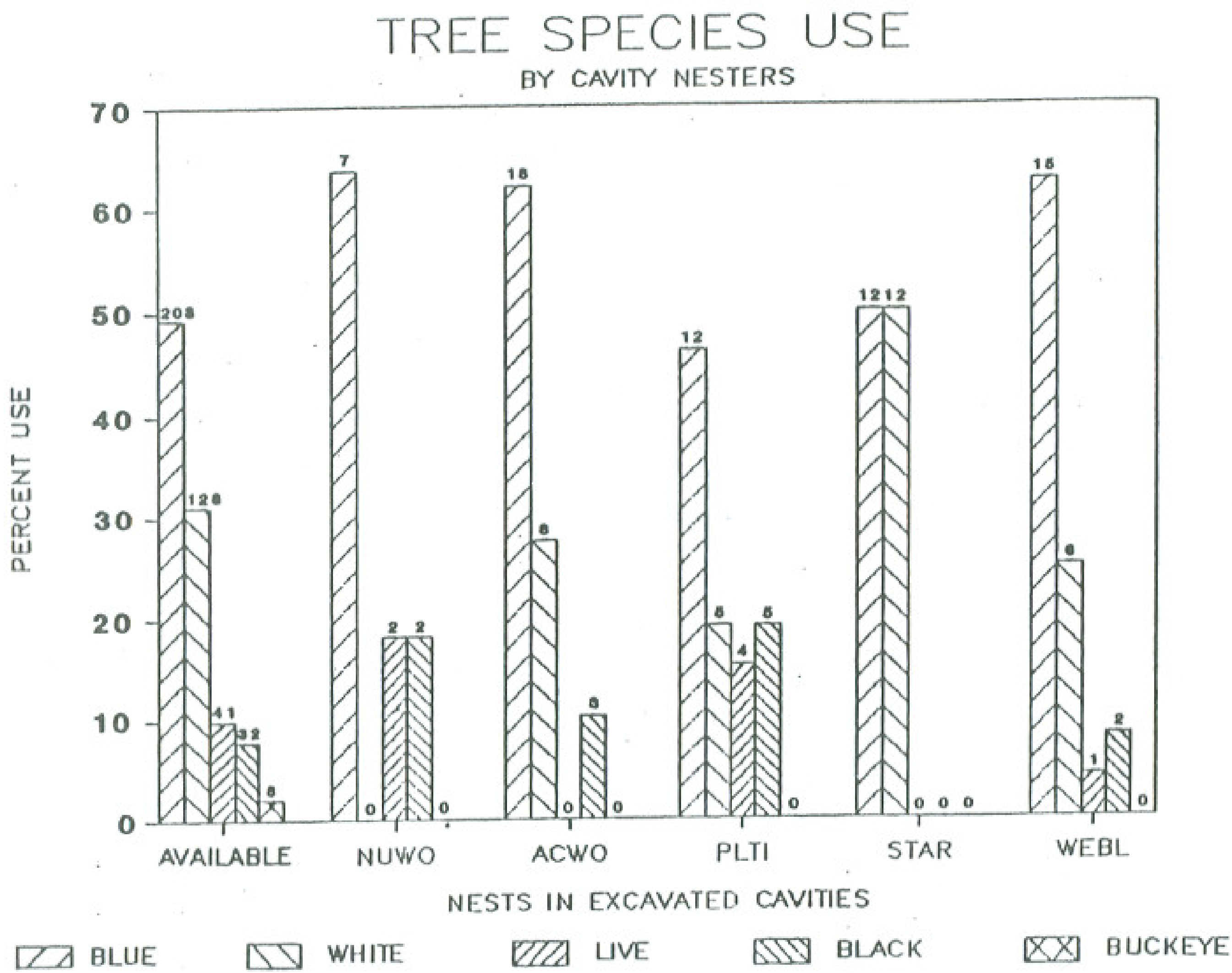


Figure 19. Nest tree selection by primary cavity nesters (Nuttall's and Acorn woodpeckers) compared to secondary cavity nesters (Plain titmouse, European starling, and Western bluebird). Sample size is indicated above bars.

cavities in tree trunks much more often than the Plain Titmouse (X^2 = 5.99, df = 1, p = 0.05).

Though excavated cavities occurred in white oaks in greater numbers than expected, we found no Nuttall's woodpecker nests in white oaks (Fig. 19). This species appeared to prefer blue oaks, evergreens and black oaks. Acorn woodpeckers however, chose blue oaks most often and white oaks in proportion to their availability (Fig. 19). The introduced European starling is feared to be a superior competitor to the Western bluebird for available cavities. Starlings used excavated cavities exclusively, with blue oak and white oak tree species chosen in equal numbers (Fig. 19). Western bluebirds chose two-thirds excavated and one-third natural cavities (Fig. 17), with blue oak being the dominant choice (> 60 percent in both cases; Fig. 18 and 19). These two potentially competing species also appeared to separate themselves temporally, with Starlings initiating nesting in late March, and Western bluebirds in mid to late April (unpublished data). We witnessed no direct competition or interference for potential nest sites between European starlings and Western bluebirds.

Violet-green swallows were the most abundant breeding species (Table 2). Our sample size for nests were small, primarily because of the late date at which they began nesting. Though arriving early in April, Violet-green swallows did not initiate their nesting cycle until early May. By this time, the Plain titmouse was already fledging young. On many occasions we observed Violet-green swallows checking cavities containing Plain titmouse nestlings. Soon after the Plain titmouse nestlings fledged, Violet-green swallows entered the cavities and begin their nesting cycle.

Of particular interest is the conspicuous absence of buckeye trees as a choice in nest selection, even though large numbers (488) of buckeye contained natural cavities. We speculate that possibly they were two low to the ground and therefore easily accessible by snakes. Gopher Snakes were seen in cavities on at least 6 occasions, and destroyed at least 3 occupied nests.

In summary, natural cavities were more abundant than excavated cavities. The seven most abundant cavity nesting species appeared to be at least partially separated in regards to nest type, tree species selection and the time at which nesting began. Of particular importance to primary cavity nesters were large size white oaks (i.e. Acorn woodpeckers) and blue oaks (i.e. Nuttall's woodpecker). For natural cavity nesters, evergreen oaks appeared to be an important source of natural cavities. Large white oaks were also chosen more than expected as granary trees by Acorn woodpeckers.

<u>Covariation of Bird Abundance and Tree Density</u>. -- One of the main objectives of our study was to investigate how the bird community varied with changes in tree density. Few species showed a simple relationship between variation in their abundance and changes in tree density. The abundance of European starling, Western bluebird, and Mourning dove all decreased with increasing tree density (Fig. 20). Brown creeper showed a positive trend of increasing numbers with tree density (Fig. 20). Plain titmouse increased strongly in number of detections up to 1000 trees/5 ha, then dropped off with increasing tree density (Fig. 21), possibly indicating a preference for moderate tree densities.

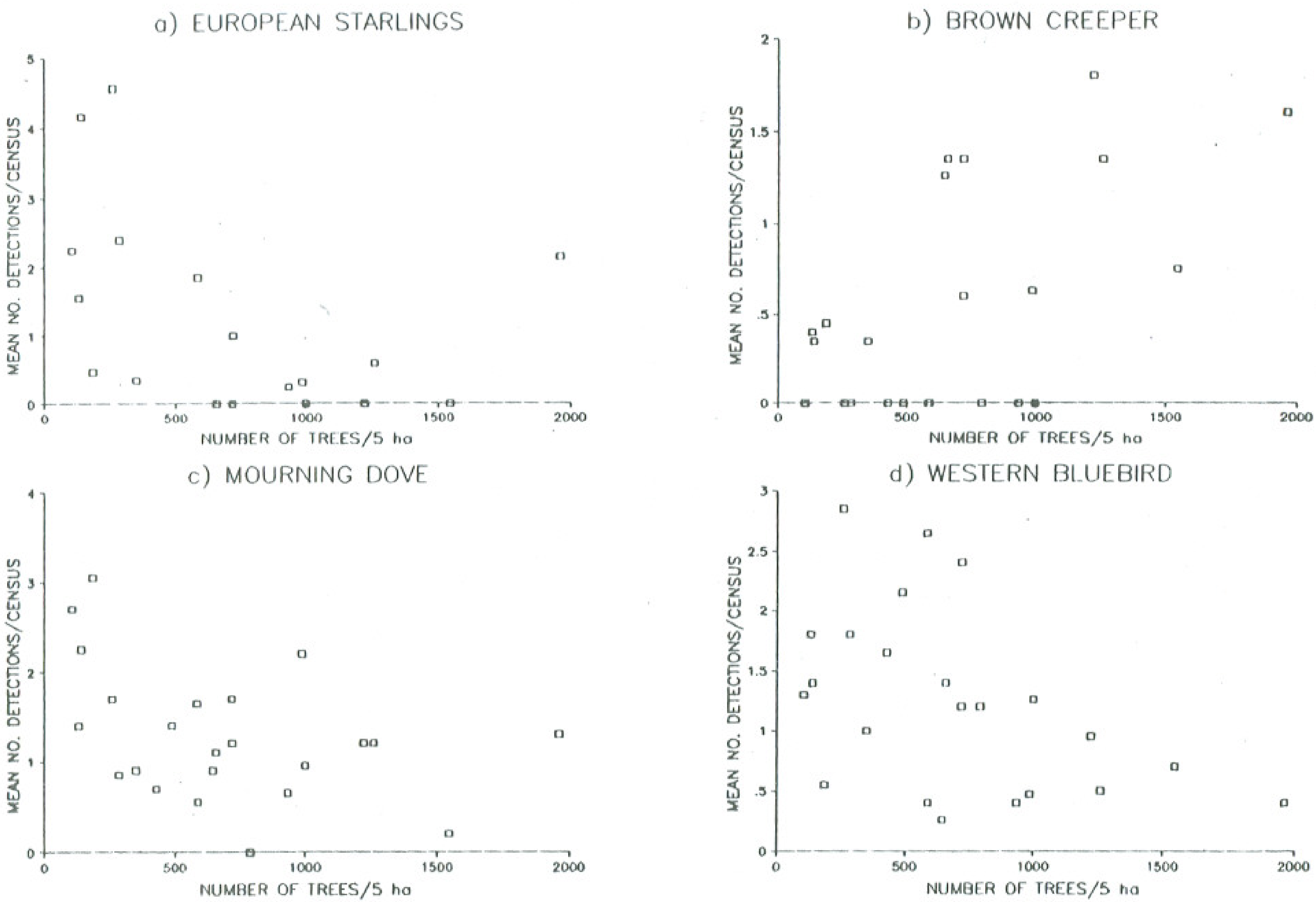


Fig. 20 Bivariate scattergrams of mean number of detections per census of 4 bird species and tree density of 23 study plots. a) European starling ($R = -0.378$, $p = 0.04$). b) Brown creeper ($R = 0.577$, $p = 0.002$). c) Mourning dove ($R = -0.512$, $p = 0.006$). d) Western bluebird ($R = -0.416$, $p = 0.012$).

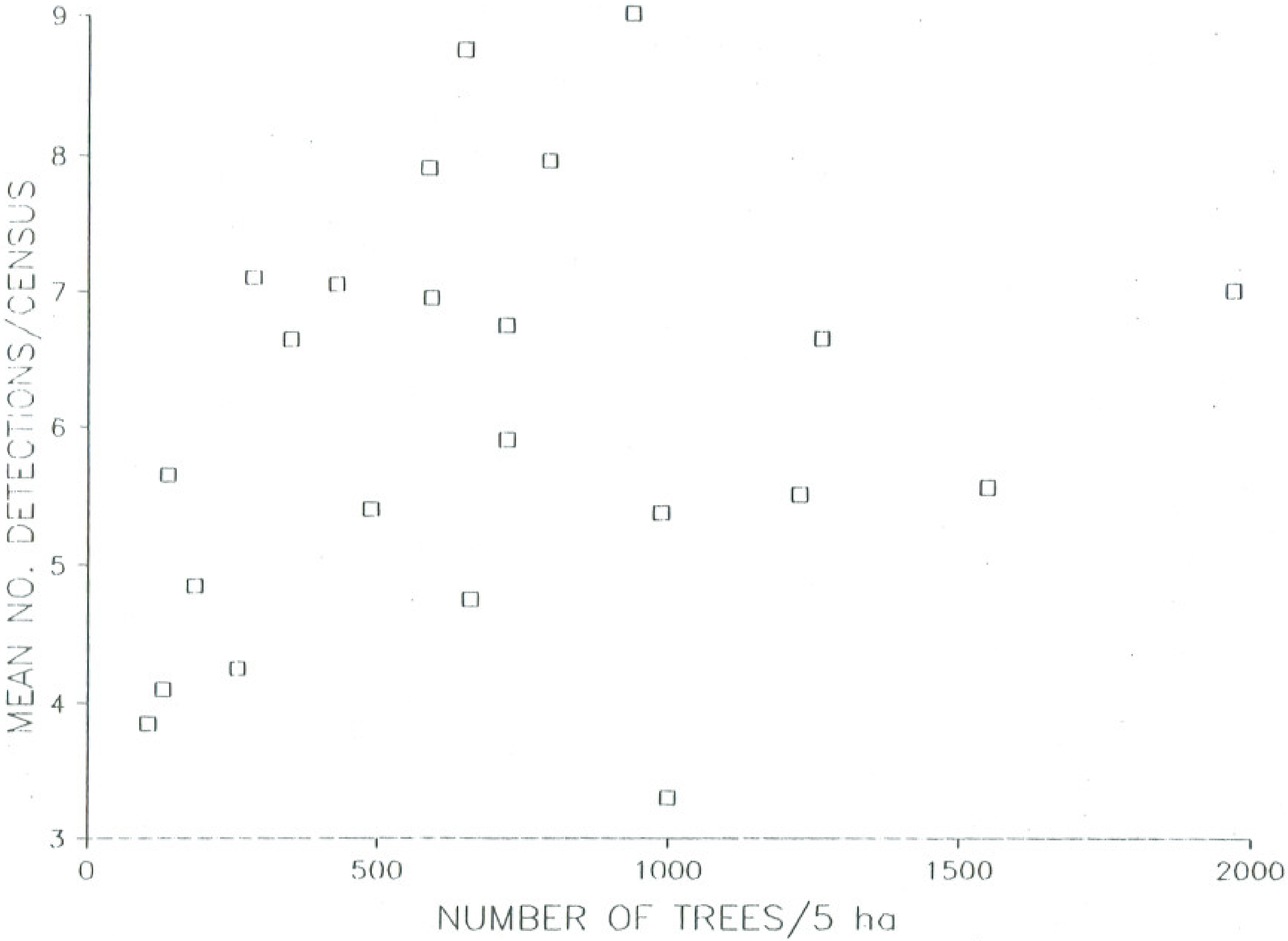
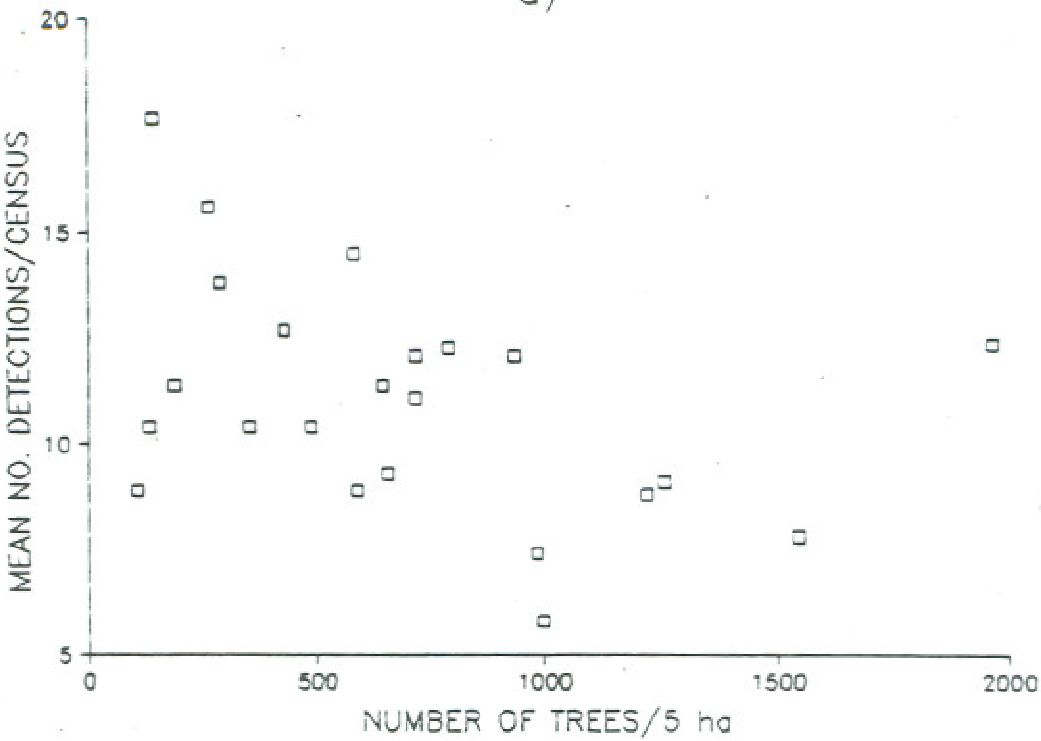


Fig. 21 Bivariate scattergram of mean number of detections per census of Plain titmouse and tree density of 23 study plots (R = 0.21, p = 0.15).

The abundance within specific bird groups showed even less covariation with tree density. The strongest relationship we detected was for secondary cavity nesters which declined in abundance with increasing tree density (Fig. 22a, R = -0.384, p = 0.035). Though significant, the magnitude of the correlation coefficient suggests that abundance within this guild covaries with features of the vegetation other than just tree density. An additional factor is that not all species comprising this guild showed a consistent response (Fig 22b). The abundance of all species decreased with increasing tree density except Plain titmouse, whose abundance increased. The regression lines in Fig. 22b are not all statistically significant, but are shown here to illustrate the point that different species within a group do not always show the same pattern of response. Other bird groups showed similar patterns of conflicting abundance trends of their component species.

Habitat Associations of Bird Groups. -- A common set of independent variables were available for selection in the regression analysis (Table 9). Approximately 56 percent of the variation in the abundance of primary cavity nesters was explained by three independent variables (Table 10). Primary cavity nester abundance varied negatively with number of snags >10 cm DBH and the abundance of buckeye trees and positively with the number of cavities. We believe the negative association with the number of snags was indirect. To explain, the number of snags varied positively with tree density and negatively with tree size. Primary cavity nesters were generally more common on study plots with sparser, larger trees with numerous a)



b)

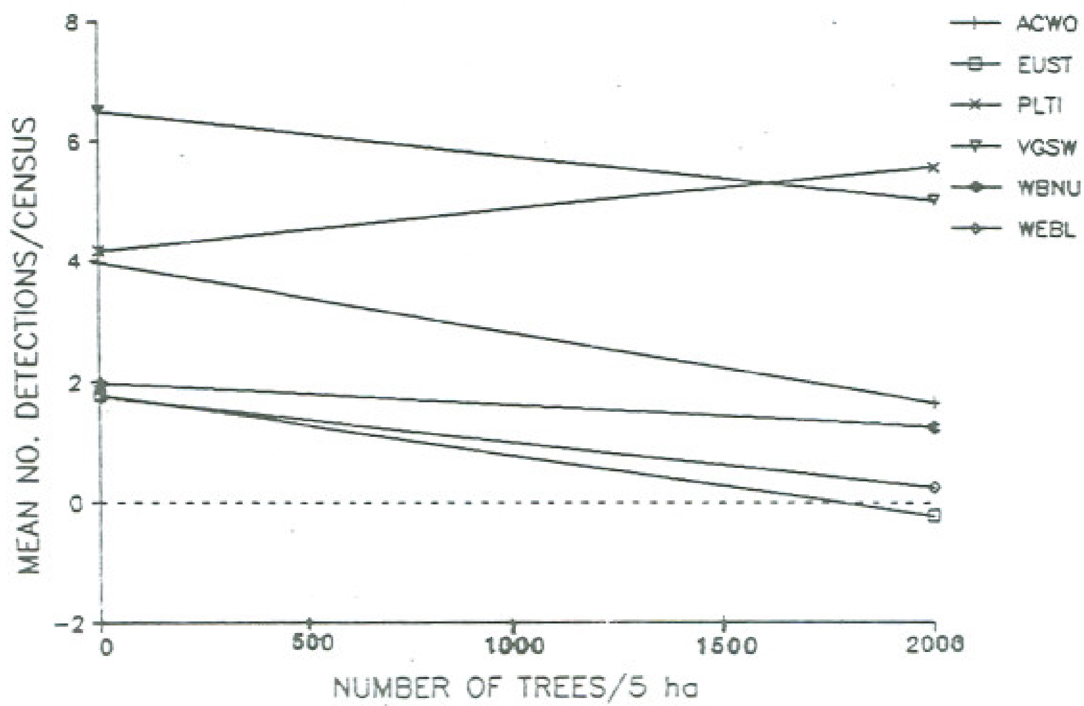


Fig. 22 Mean number of detections per census of secondary cavity nesting birds (6 species) versus number of trees per 5 hectares. a) bivariate scattergram of the mean number of detections of the guild and tree density on 23 study plots ($R = -0.384$, $p = 0.035$). b) regression lines for individual species.

Table 9. Independent variables used in regression model and transformations performed to improve their fit to a normal distribution. SQRT=square root.

VARIABLE	COUNT DATA	TRANSFORMATION
BLUE	X	SQRT(BLUE+0.5)
WHITE	X	SQRT(WHITE+0.5)
EVERGREEN	X	SQRT(LIVE+MAD+BAY+0.5)
BLACK	X	SQRT(BLACK+0.5)
BUCKEYE	X	SQRT(BUCKEYE+0.5)
SHRUB	X	SQRT(SHRUB+0.5)
DEC	X	SQRT(DEC+0.5)
CAV	X	SQRT(CAV+0.5)
CC		ARCSINE(SQRT(CC))
AVEBA		None
TREDIV		None

Table 10. Results of all possible subsets regression analyses of bird community variables regressed on vegetation variables. The independent variables and their signs are listed for each dependent variable. The "best" subset was selected on the basis of Mallow's Cp algorithm. The t-statistic is the coefficient of the variable divided by its standard error and is an indication of the contribution each variable makes to the adjusted R^2. The significance of each t-statistic (two-tailed test, df = 11) is indicated as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

DEPENDENT VARIABLE	SIGN	INDEPENDENT VARIABLE	T STATISTIC	TOTAL R^2
PRIMARY CAVITY NESTERS	-	NO. SNAGS >10cm DBH	5.25***	0.561
	-	NO. CAVITIES	5.09***	
	-	NO. BUCKEYE TREES	3.21**	
SECONDARY CAVITY NESTERS	-	NO. SHRUBS	3.04***	0.272
BARK FORAGERS	+	NO. CAVITIES	4.67***	0.642
	+	NO. WHITE OAKS	3.55**	
	-	NO. SNAGS >10cm DBH	2.81**	
	-	NO. SHRUBS	2.44*	
FOLIAGE FORAGERS	+	NO. WHITE OAKS	2.35*	0.171
GROUND FORAGERS	-	NO. BUCKEYE TREES	5.07***	0.529
AIR SALLIERS	-	NO. SNAGS >10CM DBH	2.41*	0.158
	+	NO. CAVITIES	2.05*	
CONIFER HABITAT ASSOCIATED	-	NO. BUCKEYE TREES	5.99***	0.743
	+	NO. EVERGREEN TREES	3.27**	
	-	NO. BLUE OAK TREES	3.09**	
	+	NO. BLACK OAKS	2.59*	
	-	AVERAGE BASAL AREA	2.57*	
	+	NO. CAVITIES	2.38*	
MIGRANTS	-	NO. BUCKEYE	3.67**	0.350
	-	NO. CAVITIES	2.39*	
	-	NO. SNAGS >10cm DBH	2.11*	
WINTER RESIDENTS	-	NO. BUCKEYE TREES	2.13*	0.166
	+	NO. BLACK OAKS	2.07*	

cavities. The negative association with snag density and buckeye was related to sparse stands with large trees. This nesting guild was strongly dominated by the abundance of Acorn woodpecker. Acorn woodpeckers typically excavated nest holes in large diameter branches (Mook unpublished, Univ. Calif. Santa Cruz, Santa Cruz, CA). In addition, Acorn woodpeckers stored acorns primarily in larger trees.

Only 27 percent of the variation in the abundance of secondary cavity nesters was explained by one independent variable (Table 10). Secondary cavity nester abundance varied negatively with number of shrubs. This nesting guild was more common on study plots with open understories and intermediate tree densities. The small amount of variation explained by the independent variables may be the result of the variety of life history strategies associated with members of this guild. Secondary cavity nesters vary extensively in their food resources (carnivores and insectivores), foraging strategies (salliers, gleaners, and hawkers), and foraging substrates (ground, leaf, bark, and air) which makes it difficult to characterize the habitat association of this guild.

Approximately 64 percent of the variation in the abundance of bark foragers was explained by four independent variables (Table 10). Bark forager abundance varied positively with the number of cavities and the number of white oaks. The group varied negatively with the number of snags >10 cm DBH and shrubs. Bark foragers were generally more common on study plots with a few large trees, generally white oaks and sparse understories.

The bark foraging guild was dominated by the Acorn woodpecker and the White-breasted nuthatch. The habitat association of this group was probably also related to the nest site selection and acorn storage tree characteristics associated with the Acorn woodpecker and White-breasted nuthatch. Both species typically nested in larger trees and Acorn woodpecker typically used larger diameter trees for acorn storage. The PCA of the vegetative data indicated that tree density (and therefore tree diameter) was strongly associated with variation in the number of blue oaks. This gradient contrasted dense stands of blue oak with sparse plots with large white oaks. Therefore, any species or group of species associated with larger trees is likely to also be associated with white oaks.

More than 50 percent of the variation in the abundance of ground foragers was explained by a single independent variable (Table 10). Ground forager abundance varied negatively with number of buckeye. In turn, buckeye was positively related to tree density, canopy closure, and number of shrubs. The density of buckeye was greatest on ungrazed study plots. Therefore, this guild was generally more common on study plots with sparse understories and sparser, larger trees. Plots with fewer trees and shrubs typically had a greater abundance of grasses and perhaps a greater abundance of ground-level food resources. However, ground foragers reached their greatest abundance on grazed plots suggests that tall grasses may discourage ground foraging because of the increased risk of predation. The ground foraging guild contained many (19) species representing a variety of life history characteristics, such as nest site selection (ground, open cup, and cavity). As can be seen in Table 4, the top five species in this category are American robin, Lesser goldfinch, Mourning dove, European starling, and Western bluebird. The ability to explain over half the variation in abundance with one variable suggests that food availability was an important factor influencing the abundance of this group.

Approximately 74 percent of the variation in the abundance of conifer-habitat associated species was explained by six independent variables (Table 10). The abundance of conifer-habitat associates varied positively with number of evergreen trees, black oaks, and cavities. In addition, the group varied negatively with number of buckeye, blue oak, and average basal area. Tree species diversity was typically low on study plots with large numbers of blue oaks and buckeye. Blue oak and buckeye generally dominated lower elevation plots. Conversely, tree species diversity was high on plots with many evergreen trees (which represents three tree species; live oak, madrone, and bay) and black oak. These tree species were more abundant on higher elevation plots. In general, this guild was more common on study plots with dense stands of diverse tree species typically occurring at higher elevations. The majority of species in this group were foliage foragers and air salliers (seven of 10). The habitat association of this group suggested that the abundance of sedentary and aerial prey associated with foliage may have been greater in dense stands of trees containing a variety of tree species.

Thirty-five percent of the variation in the abundance of migrant species was explained by three independent variables (Table 10). Migrant species abundance varied negatively with the number of buckeye trees, number of snags >10 cm DBH, and number of cavities. We believe the negative association with number of snags was indirect. The number of snags varied positively with tree density and negatively with tree size. Therefore, migrants were generally more common on mid- to high-elevation study plots which had sparse to intermediate tree densities. This group was represented by a number of species with similar abundances but widely varying life history strategies. However the association with larger trees suggests that larger, taller trees may offer greater food abundance during the period of migration. Alternatively, this group may have been keying into higher elevation plots, which typically had greater tree species diversity and larger trees.

Habitat Associations of Selected Bird Species. -- Variations in the abundance of 11 individual bird species (the 10 most abundant bird species and an additional cavity excavator) were analyzed using all possible subsets regression to investigate their relationships with variation in the vegetative characteristics of the study plots. The same 11 vegetation variables were used as independent variables for these analyses as were used for analysis of the bird groups (Table 9).

Approximately 56 percent of the variation in the abundance of Acorn woodpecker was explained by three independent variables (Table 11). Acorn woodpecker abundance varied positively with number of cavities and negatively with number of snags >10 cm DBH and number of buckeye trees. Large trees, primarily white oak, served as the primary site for nests and acorn storage.

More than 42 percent of the variation in the abundance of Nuttall's woodpecker was explained by three independent variables

Table 11. Results of all possible subsets regression analyses of bird species abundances regressed on vegetation variables. The independent variables and their signs are listed for each dependent variable. The "best" subset was selected on the basis of Mallow's Cp algorithm. The t-statistic is the coefficient of the variable divided by its standard error and is an indication of the contribution each variable made to the adjusted R^2. The significance of the t-statistic (two-tailed, df = 11) is indicated as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

DEPENDENT VARIABLE	SIGN	INDEPENDENT VARIABLE	T STATISTIC	TOTAL R^2
PLAIN TITMOUSE	-	NO. SHRUBS	3.06**	0.563
	+	NO. BUCKEYE TREES	2.59*	
	+	NO. CAVITIES	2.32*	
ACORN WOODPECKER	-	NO. SNAGS >10cm DBH	5.31***	0.556
	+	NO. CAVITIES	4.89***	
	-	NO. BUCKEYE TREES	3.14**	
NUTTALL'S WOODPECKER	+	NO. CAVITIES	3.10**	0.427
	+	NO. WHITE OAK TREES	3.01**	
	-	NO. SNAGS >10cm DBH	2.98**	
WHITE-BREASTED NUTHATCH	-	NO. EVERGREEN TREES	3.03**	0.419
	+	AVERAGE BASAL AREA	2.76**	
	+	NO. CAVITIES	2.64*	
	+	CANOPY CLOSURE	2.21*	
	+	NO. WHITE OAKS	1.96*	
WESTERN BLUEBIRD	-	NO. EVERGREEN TREES	2.07*	0.325
	-	NO. BUCKEYE TREES	1.99*	
EUROPEAN STARLING	+	AVERAGE BASAL AREA	4.01**	0.407
VIOLET-GREEN SWALLOW	+	CANOPY CLOSURE	3.34**	0.384
	+	NO. BUCKEYE TREES	2.68*	
	-	NO. EVERGREEN TREES	2.64*	
	+	AVERAGE BASAL AREA	2.23*	
SCRUB JAY	-	NO. SNAGS >10cm DBH	4.05***	0.472
	+	NO. BUCKEYE TREES	3.01**	
	+	CANOPY CLOSURE	2.12*	
	+	WHITE OAKS	2.10*	
MOURNING DOVE	-	NO. BUCKEYE TREES	3.61**	0.354
AMERICAN ROBIN	+	NO. EVERGREEN TREES	2.90**	0.407
	-	NO. SHRUBS	2.88**	
	-	NO. BUCKEYE TREES	2.69*	
LESSER GOLDFINCH	-	TREE DIVERSITY	2.67*	0.220

(Table 11). Nuttall's woodpecker abundance varied positively with the number of white oaks and cavities and negatively with the number of snags >10 cm DBH. This bird species was generally more common on study plots with a few large trees, white oaks in particular. The habitat association of Nuttall's woodpecker does not reflect the choice of nest tree species shown in earlier analyses. We found no Nuttall's nesting in white oaks. Rather, they used blue oak, black oak, and evergreen trees for nesting.

The habitat association of Nuttall's woodpecker was very similar to that described for Acorn woodpecker. In addition, they co-occurred on all but one of our study plots. However the characteristics of their nests differed. Nuttall's woodpecker selected tree species for nest sites, at a different frequency, and, in addition, nested in significantly ($p<0.01$) smaller diameter branches than Acorn woodpeckers (Mook pers. comm.). We observed Acorn woodpeckers exhibiting aggressive behavior toward Nuttall's woodpecker on several occasions. At one Nuttall's nest, a pair of Acorn woodpeckers appeared to displace an adult feeding nestlings and to attempt to injur the nestlings by jabbing their bills into the nest cavity. This harassment continued for nearly two weeks. Perhaps Acorn woodpecker and Nuttall's woodpecker were potential competitors and the apparently dominant, aggressive behavior of the Acorn woodpecker caused the Nuttall's woodpecker to choose different tree species and smaller substrates for nesting to reduce the frequency and/or intensity of conflicts between the two species.

Approximately 42 percent of the variation in the abundance of White-breasted nuthatch was explained by five independent variables (Table 11). White-breasted nuthatch abundance varied positively with average basal area, canopy closure, cavities, and white oaks; and negatively with number of evergreen trees. This species was generally more common on study plots with larger trees with white oak as a component, and few ravines, which were typically densely vegetated with evergreens. White-breasted nuthatches typically nested in large diameter trees, partially explaining the observed habitat association.

More than 56 percent of the variation in the abundance of Plain titmouse was explained by three independent variables (Table 11). Plain titmouse abundance varied positively with the number of buckeye trees and cavities and negatively with the number of shrubs. This species was generally more common on study plots with many trees with numerous cavities and few shrubs. Plain titmouse foraged primarily on foliage and appeared to use a wide range of diameters of trunks and branches for nesting. Therefore, denser stands of trees may have offered a greater abundance of both nest sites and prey. Martin and Karr (in press) argue that nest predation is decreased in areas which have a greater number of potential nest sites, because it becomes energetically more expensive for predators to locate occuppied nests. Perhaps an additional benefit of denser stands may be the increased number of potential nest sites.

Approximately 41 percent of the variation in the abundance of European starling was explained by one independent variable (Table 11). Starling abundance varied positively with average basal area.

That is, starlings were more common on study plots with a few large trees. This habitat pattern is similar to that of the Acorn woodpecker, and we often observed starlings nesting in cavities previously excavated by Acorn woodpeckers.

Western bluebird abundance varied negatively with number of evergreen trees and buckeye (R^2 = 0.325, Table 11). Evergreen trees and buckeye in turn, varied positively with canopy closure. Collectively these variables describe the dense stands of vegetation that were most often confined to ravines. In addition, the ground cover under evergreen trees was typically sparse because of extensive shading and leaf fall. Therefore, Western bluebirds were generally more common on study plots with open canopies, away from ravines, and with a greater density of grasses. This habitat pattern is alligned with the species behavior of obtaining prey from the ground by sallying.

Violet-green swallow abundance varied positively with canopy closure, average basal area, and the number of buckeye trees, and varied negatively with number of evergreen trees (R^2 = 0.384, Table 11). In turn, buckeye and canopy closure varied positively with number of blue oaks. Therefore, Violet-green swallow was generally more common on study plots with many buckeye trees and large blue oaks. As discussed in earlier analyses, Violet-green swallow often occuppied recently vacated Plain titmouse nests. Indeed the habitat associations of the two species were very similar. However the foraging behaviors of the two species differed. Violet-green swallow foraged by hawking insects. Plain titmouse foraged primarily on foliage while feeding nestlings, and mossy branches and the ground after the young fledged (unpublished data). Perhaps denser stands with blue oaks not only provided abundant nest sites for both species, but also a sequence of abundant prey types.

Mourning dove abundance varied negatively with the number of buckeye trees (R^2 = 0.354, Table 11). Mourning dove abundance was also positively correlated with average basal area and negatively correlated with the number of blue oak trees. This species was generally more common on study plots with a few large trees other than blue oaks. Mourning doves typically built open nests on tree limbs and foraged on the ground. Large trees may provide more abundant suitable nest sites and the lack of canopy cover may provide greater food availability.

Almost 50 percent of the variation in the abundance of Scrub jay was explained by variation in canopy closure, the number of buckeye trees and the number of white oaks and the number of snags >10 cm DBH. The positive association with canopy closure and the negative association with the number of snags (and therefore few large trees) suggests that Scrub jays were generally more common on study plots with a clumped distribution of trees. Buckeye were often associated with the moister environment of ravines and white oaks were typically associated with upland areas. The habitat association would result from the presence of densely vegetated ravines in otherwise less dense stands of trees with white oak as a component.

American robin abundance varied positively with the number of evergreen trees and negatively with the number of buckeye trees and shrubs (R^2 = 0.407, Table 11). In addition, American robin abundance had positive, but nonsignificant, relationships with average basal area and white oaks. American robins were generally more common on study plots with open understories and a few large trees. In addition, these plots often contained ravines vegetated by dense evergreen trees. American robin typically foraged on the ground in open areas and often took refuge in nearby dense vegetation when disturbed.

Multivariate Patterns. -- We have plotted the location of the 10 most abundant species and the nine guilds in the three-dimensional vegetation space (Fig. 23). Because all points, except the European starling, fell very near the origin (0,0,0), we have simply indicated this location by a star. A common location for all these points indicates that species or guild abundance did not vary systematically with the ordination scores. This occurred despite the fact that most species and guilds showed substantial abundance variation across plots (coefficients of variation > 40 percent). The weighted locations near the origin indicate that none of the guilds or most abundant species found optimal conditions at the extremes of any vegetative gradient.

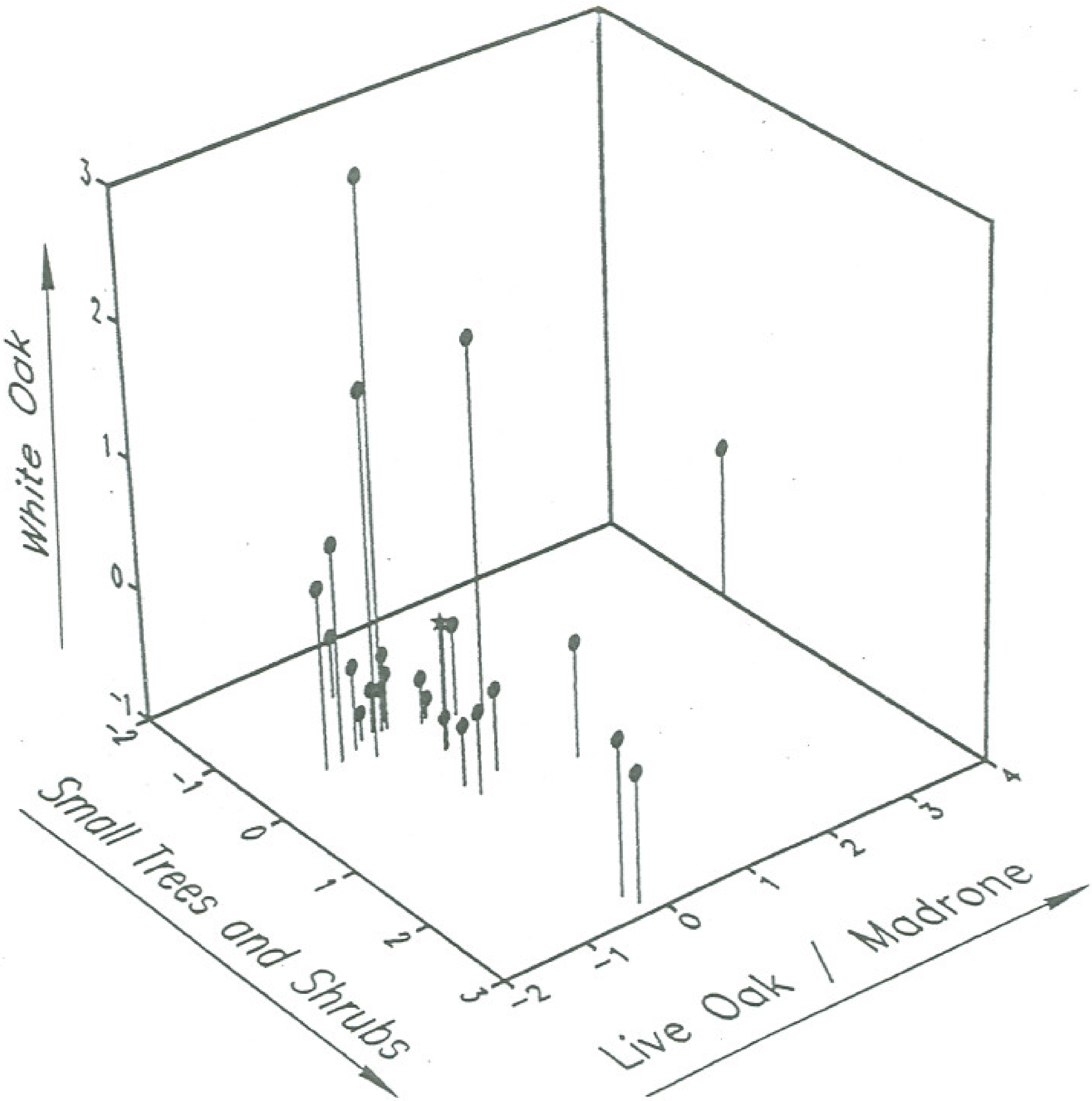


Figure 23. Ordination of the 23 study plots along the first three principal components. Axis I represents variation in the number of small trees and shrubs per plot, axis II the number of live oak and madrone trees per plot, and axis III the number of white oak trees per plot. The star (★) in the figure indicates the approximate, weighted location of the 10 most abundant bird species in this vegetation space.

DISCUSSION

General Bird Community Patterns

The results of our study have supplied additional confirmation of the high number of breeding bird species in California oak woodlands (see review in Verner 1980). Based on the criteria of territorial defense, our data suggest that at least 49 species of birds bred at the Hopland Field Station in the years 1986, 1987. A comparison of our results with those based on Breeding Bird Censuses published in American Birds indicates that our study area is in the upper 10 percent of habitat types in the continental United States in terms of species richness. Our density estimates are less reliable than the majority of those published in American Birds because of our small plot sizes and the fact that we were not able to use a territory mapping procedure. Verner (1980) has shown that small plot sizes can lead to large positive biases in the estimate of breeding bird density. However, if we assume that our census methodology provided perfect detection out to 50 m on either side of the transect and that all detections represented territorial birds, we can compare our density estimates with other habitat types in the continental United States. When we do this we observe that the breeding density in oak woodlands is in the upper 25 percent of habitat types. Collectively, these statistics indicate the high relative importance of California oak woodlands to United States avifauna.

The 12 cavity-nesting species composed a substantial proportion of the breeding bird community (25 percent) and the total breeding density (58 percent) on our study plots. Our estimate of the relative importance of cavity-nesting species is comparable to conifer dominated habitats across the western U. S. (Scott et al. 1980, Raphael 1981). However, our estimates of the relative density of cavity-nesters is considerably higher than most (Scott et al. 1980). To a large extent the dominance of cavity nesters on our plots was attributable to our density estimates for the Violet-green swallow. In addition to the significance of cavity-nesting species, our multivariate analyses suggest that species whose distributional centers lie to the north of Hopland (conifer associates) and a composite group of migrant and resident species are also significant components of these communities.

Our study plots were arranged along a steep elevational gradient, varying from 200 - 1000 m. Abiotic variables that varied in parallel with the elevational gradient affected the vegetative community which in turn, affected the structure of the bird community. A regression of migrant species abundance on elevation showed a strong increase with increasing elevation. We believe this pattern was attributable to the increased importance of plant species characteristic of the mixed-evergreen community (e.g., madrone, black oak, Oregon white oak, bay) at the higher elevation plots. The distributional center of this plant community lies to the north of Hopland and many of the bird species associated with this habitat are near their southern distributional limits. In addition, there was an increase in bird species richness with elevation, probably attributable to the accumulation of an increasing number of migrants on the higher plots.

Vegetative Communities

We did not randomly sample available habitats at the Hopland Field Station. Rather, we sampled systematically so that our study plots would represent a smooth, but steep, gradient in oak tree density. As a consequence we cannot make inferences to relative proportions nor general characteristics of all the vegetative communites at the field station. However, we believe that our study plots samples a range of vegetative conditions and are representative of much of the variation at the site.

A primary, but unresolved, issue concerns the definition of the oak woodland community. For example, is there more than one vegetative community represented in our sample of 23, 5 ha plots? Apparently, the answer to this question is unknown. The woodlands at the Hopland Field Station are heterogeneous both in species compositon and the spatial pattern of the vegetation, and there are no discrete boundaries separating various woodland habitats. From the principal components analysis of the vegetative censuses from each plot, we detected several significant and independent gradients of variation. The dominant gradient represented variation in tree density and simply reflected our sampling design. However, we detected other significant gradients representing variation from evergreen species to deciduous oaks and from predominantly blue oak plots to white oak and bay plots. In addition, study plots which included ephemeral streams (ravines) contained greater numbers of buckeye trees, and plots at higher elevations had greater numbers of black oaks. There was a moderate degree of vegetative variation within some our 5 ha study plots.

Within plot habitat heterogeneity, however, was masked in our analyses. Because we completely censused the vegetation on each study plot, each study plot was represented by a single datum in the analyses.

Our samples, based on plot sizes of 5 ha, were characterized by both within and among plot variation. Because of the heterogeneity of northern oak woodlands, we were, and continue to be, uncertain as to the correct spatial scale for sampling and anaysis. For small scale changes in plant species, such as caused by ephemeral streams, 5 ha plots may have been too large. However, to sample the variation that is representative of the oak woodland as a functioning ecosystem may require study plots >> 100 ha in size. Below we discuss the issue of sampling scale as it applies to the strength of the bird/habitat relationships that we observed.

Bird/Habitat Relationships

Given the number of cavity-nesting species and their numerical dominance in these communities, it seems appropriate to focus on the availability of their potential nest sites. The majority of both natural and excavated cavities were found in blue oak trees. However, this pattern was expected based on their relative availability. In contrast, a much greater than expected number of natural cavities occurred in evergreen tree species, primarily live oak. Also, a much greater than expected number occurred in white oaks, primarily in valley oak. When the distribution of both natural and excavated cavities are examined as a function of tree diameter, a consistent pattern arises. For almost all tree species, the number of both cavity types is strongly related to tree size. Presumably this occurs for two primary reasons. Larger trees are generally older and have thus had greater time to accumulate cavities. Also older trees are more likely to have experienced loss of limbs and disease, two factors which promote natural and excavated cavities.

The importance of limb loss followed by diseases which affect the heartwood of trees has been demonstrated for a variety of cavity-nesting species. Conner et al. (1976) cut down woodpecker nest trees in an oak-hickory forest and examined the wood around the cavity for fungal activities associated with wood decay. All 24 trees examined were infected with heart rot fungi that had softened the core of the nest tree. Further, they found that many of the cavities were located immediately below an "old stub of dead, broken branch". Miller and Miller (1980) found results very similar to those of Conner et al. (1976). After cutting down 44 nest trees of eight excavator species, they found that 42 of the nest holes were placed in decayed heartwood.

Both natural and excavated cavities are important to cavity-nesting species at Hopland. For example, the Acorn and Nuttall's woodpeckers exclusively used excavated cavities, European starling and Western bluebird used primarily excavated cavities and, all secondary cavity nesters used excavated cavities to some degree. Acorn woodpeckers are a particularly important species as they are the primary source of excavated cavities for subsequent use by secondary cavity-nesting species.

The majority (65 percent) of secondary cavity nests occurred in natural cavities, and some species, such as Plain titmouse and White-breasted nuthatch, used natural cavities almost exclusively. The extent to which natural cavities were used for nesting by secondary cavity-nesters was high compared to another oak woodland in California. The secondary cavity-nesters at San Joaquin Experimental Range (Madera County) used natural cavities 34 percent of the time (J. Waters, unpublished data, Humboldt State University, Dept. of Wildlife, Arcata, California). Collectively, these results suggest that large, old trees of both deciduous and evergreen oaks are important to meet the needs of primary cavity-nesters for nest substrates and secondary cavity-nesters for natural cavities as well as excavated cavities.

An additional argument for the importance of large trees is provided by the distribution of Acorn woodpecker granary trees. They were concentrated in the large deciduous oaks, averaging over 75 cm in diameter in the most frequently used tree species (blue oaks and white oaks). In addition to the demonstrated value of large trees, our data also indicate that a diversity of tree species is important to the cavity-nesting guild. We found nests in four or more tree species for all cavity-nesting species. Further, the distribution of nests by tree species, for both natural and excavated cavities, varied among the guild members.

Our study plots were selected to reflect a gradual, but extensive, variation in tree density. Given this sampling design, it is logical to ask how bird species responded to variation in this single variable. With a few exceptions, we failed to detect simple relationships between species abundance and varying tree density. The exceptions were Western bluebird, European starling, and Mourning dove which responded negatively to increasing tree density, and the Brown creeper which responded positively. We also looked for a relationship between abundance within a guild and tree density. The strongest pattern we detected was a negative relationship between the abundance of secondary cavity-nesters and tree density. Of interest, not all the guild members showed a constant response: Plain titmouse actually increased in abundance with tree density.

There were a number of species with overall low abundances that appeared to be most abundant on dense plots. Pygmy owl families (n = 8), Barn owl nests (n = 2), and Turkey nests (n = 2) were found on dense plots only. These species may have responded to the reduced disturbance resulting from less intense grazing on dense plots (F. Lyle, pers comm., Hopland Field Station, Hopland, California). Dense plots were not grazed as heavily because of the reduced amount of forage they produced.

To understand why few species or guilds showed a relationship to tree density it is important to realize that tree density did not vary independently of other habitat features. For example, areas with high tree density tended to be occupied by stands of blue oak trees with small average diameters, with low and closed canopies, dense shrubs, and many snags. Areas of lower tree densities had much larger trees, greater dominance of valley oak, more open canopies, and few shrubs or snags. That is, both structural and flouristic features of the vegetation covaried with tree density.

An additional factor contributing to the lack of a simple relationship between bird abundance and tree density is that few of our study plots were characterized by a uniform distribution of trees. Rather, the trees were distributed in a patchy fashion across the plot. Our estimate of tree density for each plot contained no information about the distributional pattern of trees on the plot. We believe that birds respond to the spatial pattern of the vegetation as well as its average values.

We attempted to established plots in areas of uniform tree distribution, but this was generally not possible. The reason is that oak woodlands are characterized by a heterogeneous distribution of their trees. The mosaic nature of the woodland landscape makes it difficult to determine the appropriate spatial scale to sample in order to study the dynamics of the system. The 5 ha size of our study plots represented a compromise between the minimum size needed for accurate estimates of the bird community and a sufficient sample size to detect at least strong bird/habitat associations. It is quite possible that most of the bird species breeding in oak woodlands respond to the habitat at a variety of spatial scales. We believe that these scales could range from a suitable nest site in an individual tree, to the size of the patch in which that tree is found, to the juxtaposition of that patch to other patches in the landscape. Further complicating the system is that each species may have its own unique scales of response to habitat variation. To an unknown degree, our results were affected by the scale at which we sampled both the bird and vegetative communities.

We examined patterns of covariation between bird species and components of the vegetation with regression analyses. For several bird guilds and individual species we found significant models which explained > 50 percent of their abundance variation. These results suggest a rather strong association between bird abundance and habitat structure and flouristics. Interpretation of regression models must be done cautiously because few variables in these models vary independently of other vegetation variables. For example, several models contained the variable, number of snags > 10 cm DBH. However, this variable was strongly related to habitats with a high density of small diameter trees and closed canopies. We believe it was this habitat condition, rather than the number of snags per se, that was associated with variation in bird abundance.

An additional example is the variable, number of cavities, which was selected in the regression models for four cavity-nesting species (Acorn woodpecker, Nutttall's woodpecker, Plain titmouse, and White-breasted nuthatch). Number of cavities covaried positively with the density of all tree species, particularly with the number of blue and live oaks. In light of the positive association of cavity-nesters with larger diameter trees, this result suggests that these cavity-nesters find optimal habitat in areas with intermediate tree densities. Intermediate tree densities may provide an abundance of food resources, as well as large enough diameter trees to provide an adequate abundance of nest cavities. In addition, at least five different tree species were significant independent variables in one or more of the regression models. This results suggests that the tree species diversity of these woodlands contributed to the high bird species richness we observed.

Very little separation of bird species or guilds was observed when plotted in the three-dimentional vegetation space. This indicates that species or guild abundance did not vary systematically with the vegetative ordination of the study plots. This is not a consequence of low variation in abundance; most species had coefficients of variation > 40 percent. The simplest interpretation of this result is that it reflects the sampling problems discussed above. In general, much of the vegetative variation on a plot was masked by considering each plot as a single data point in the analyses. Strong covariation between bird abundance and vegetation was not detected until the vegetation variables were examined individually in the regression analyses.

The observation that no guild nor any of the most abundant species found optimal conditions at the extremes of any vegetative gradient may be important. This result may give insight into the spatial scale at which birds were responding to the oak woodland environment. Plots that differed widely in vegetative structure (e.g., tree density) did not consistantly covary with abundance. This result suggests that bird species were responding to their environment at spatial scales much greater than 5 ha.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

(1) Cavity-nesting species compose 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 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 (> 55 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 the 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 vegetative variables. Among these were seven species of hardwood trees. These results suggest that a high tree species richness is important to oak woodland birds.

(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 integrety of the breeding bird community, we recommend maintaining a variety of tree densities.

(8) Several bird species were positively associated with vegetation restricted to the borders of ephemeral streams. We recommend that these ephemeral stream corridors be free of disturbance and that grazing be minimized in these areas.

(9) Oak woodlands are very diverse in terms of the spatial distribution 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 100 ha as the minimum size of a management unit.

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Appendix A. Correlation coefficients between 22 vegetation variables representing the vegetative characteristics across all study plots.

	BLUE1	BLUE2	BLUE3	BLUE4	WHITE1+2	WHITE3	BLACK1	BLACK2	BLACK3	LIVE1	LIVE2	LIVE3	BUCKEYE
BLUE1	1.00												
BLUE2	0.81	1.00											
BLUE3	0.39	0.76	1.00										
BLUE4	0.22	0.36	0.61	1.00									
WHITE1+2	-0.32	-0.15	-0.24	-0.52	1.00								
WHITE3	-0.31	-0.54	-0.71	-0.87	0.69	1.00							
BLACK1	0.59	0.60	0.35	0.06	0.01	-0.23	1.00						
BLACK2	0.16	0.29	0.32	-0.02	0.00	-0.13	0.72	1.00					
BLACK3	0.00	0.05	0.03	-0.18	0.14	0.11	0.27	0.74	1.00				
LIVE1	0.67	0.75	0.55	0.14	0.02	-0.32	0.76	0.41	-0.09	1.00			
LIVE2	0.22	0.30	0.21	-0.08	0.11	0.01	0.25	0.19	-0.07	0.52	1.00		
LIVE3	-0.21	-0.31	-0.44	-0.39	0.07	0.41	-0.09	-0.04	0.04	-0.11	0.60	1.00	
BUCKEYE	0.20	0.30	0.44	0.42	-0.14	-0.36	0.48	0.48	0.09	0.37	0.10	-0.16	1.00
MADRONE	-0.14	-0.06	-0.15	-0.34	0.27	0.29	0.03	0.24	0.42	0.01	0.66	0.70	-0.11
BAY	-0.01	-0.10	-0.31	-0.57	0.56	0.69	0.08	-0.06	-0.11	0.11	0.37	0.47	-0.07
BAMAD	-0.11	0.02	-0.07	-0.25	0.14	0.18	0.15	0.38	0.53	0.05	0.59	0.65	-0.03
BABUCK	0.30	0.34	0.48	0.46	-0.14	-0.36	0.43	0.42	0.08	0.37	0.19	-0.11	0.96
BALIVE	0.01	-0.06	-0.23	-0.28	0.06	0.25	0.06	-0.02	-0.08	0.17	0.77	0.93	-0.09
AVEBA	-0.42	-0.69	-0.81	-0.46	-0.06	0.45	-0.38	-0.38	-0.17	-0.51	-0.33	0.38	-0.43
TOTALBA	0.31	0.37	0.42	-0.08	0.41	0.14	0.37	0.38	0.25	0.50	0.70	0.43	0.28
CC	0.58	0.75	0.71	0.27	0.11	-0.33	0.57	0.42	0.15	0.72	0.63	0.06	0.39

	MADRONE	BAY	BAMAD	BABUCK	BALIVE	AVEBA	TOTALBA	CC
MADRONE	1.00							
BAY	0.23	1.00						
BAMAD	0.98	0.15	1.00					
BABUCK	-0.10	-0.04	-0.04	1.00				
BALIVE	0.68	0.41	0.61	-0.02	1.00			
AVEBA	-0.06	0.01	-0.09	-0.47	0.22	1.00		
TOTALBA	0.54	0.49	0.52	0.34	0.57	-0.45	1.00	
CC	0.28	0.16	0.32	0.47	0.29	-0.74	0.79	1.00

Appendix B. Occurrence of natural and excavated cavities in different tree species at Hopland, California.

Cavity Type[a]	Plant group[b]	Total available	Proportion of total	Number observed	Proportion of observed	95% C.I. on proportion of observed[c]	Significance[d]
NATURAL CAVITIES-minor	BLUE OAK	10,740	0.67	696	0.39	$0.36 < p < 0.41$	lesser
	WHITE OAK	1,505	0.09	211	0.12	$0.10 < p < 0.14$	greater
	EVERGREEN	1,895	0.12	382	0.21	$0.19 < p < 0.26$	greater
	BLACK OAK	618	0.04	133	0.07	$0.06 < p < 0.09$	greater
	BUCKEYE	1,308	0.08	385	0.21	$0.19 < p < 0.24$	greater
NATURAL CAVITIES-major	BLUE OAK	10,740	0.67	145	0.36	$0.30 < p < 0.42$	lesser
	WHITE OAK	1,505	0.09	61	0.15	$0.10 < p < 0.20$	greater
	EVERGREEN	1,895	0.12	106	0.26	$0.21 < p < 0.32$	greater
	BLACK OAK	618	0.04	35	0.09	$0.05 < p < 0.12$	greater
	BUCKEYE	1,308	0.08	53	0.13	$0.09 < p < 0.17$	greater
EXCAVATED CAVITIES-minor	BLUE OAK	10,740	0.67	151	0.48	$0.40 < p < 0.55$	lesser
	WHITE OAK	1,505	0.09	91	0.29	$0.22 < p < 0.35$	greater
	EVERGREEN	1,895	0.12	35	0.11	$0.06 < p < 0.16$	
	BLACK OAK	618	0.04	24	0.08	$0.04 < p < 0.12$	
	BUCKEYE	1,308	0.08	8	0.03	$0.00 < p < 0.05$	lesser
EXCAVATED CAVITIES-major	BLUE OAK	10,740	0.67	52	0.50	$0.37 < p < 0.63$	lesser
	WHITE OAK	1,505	0.09	37	0.36	$0.24 < p < 0.48$	greater
	EVERGREEN	1,895	0.12	6	0.06	$0.00 < p < 0.12$	
	BLACK OAK	618	0.04	8	0.08	$0.01 < p < 0.15$	
	BUCKEYE	1,308	0.08	0	0.00	----- -----	lesser

[a] minor, 1-3 cavities; major, > 3 cavities.

[b] Species composition of plant groups: BLUE OAK = Quercus douglasii; WHITE OAK = Q. lobata and Q. garryana; EVERGREEN = Q. wislizenii, Q. agrifolia, Q. chrysolepis, Umbellularia californica, and Arbutus menzesii; BLACK OAK = Q. kellogii and Q. morehus (Oracle oak); BUCKEYE = Aesculus californicus.

[c] Bonferoni confidence intervals (Neu et al. 1974).

[d] Significance determined when proportion of total falls outside 95% C.I. of proportion of observed.

Appendix C. Occurrence of granaries in different tree species at Hopland, California.

Level[a]	Plant group[b]	Total available	Proportion of total	Number observed	Proportion of observed	95% C.I. on proportion of observed[c]	Significance[d]
ACORN	BLUE OAK	10,740	0.67	147	0.55	0.47 <p< 0.63	lesser
STORAGE	WHITE OAK	1,505	0.09	65	0.27	0.18 <p< 0.31	greater
TREES-	EVERGREEN	1,895	0.12	18	0.07	0.03 <p< 0.11	lesser
minor	BLACK OAK	618	0.04	22	0.08	0.04 <p< 0.13	
	BUCKEYE	1,308	0.08	12	0.05	0.01 <p< 0.08	
ACORN	BLUE OAK	10,740	0.67	22	0.47	0.28 <p< 0.65	lesser
STORAGE	WHITE OAK	1,505	0.09	19	0.40	0.22 <p< 0.56	greater
TREES-	EVERGREEN	1,895	0.12	2	0.04	0.00 <p< 0.12	
major	BLACK OAK	618	0.04	1	0.02	0.00 <p< 0.08	
	BUCKEYE	1,308	0.08	3	0.06	0.00 <p< 0.15	

[a] minor = < 10% of tree used for acorn storage; major = > 10% of tree used for acorn storage

[b] see Appendix B.

[c] Bonferoni confidence intervals (Neu et al. 1974).

[d] significance determined when proportion of total falls outside 95% C.I. of proportion of observed.

Appendix D. Occurrence of Plain titmouse and White-breasted nuthatch nest cavities in different tree species at Hopland, California.

Bird species-cavity type	Plant group[a]	Total available	Proportion of total	Number observed	Proportion of observed	95% C.I. on proportion of observed[b]	Significance[c]
PLAIN	BLUE OAK	203	0.49	12	0.50	0.25 <p< 0.75	
TITMOUSE	WHITE OAK	128	0.31	5	0.30	0.07 <p< 0.53	
NESTS-	EVERGREEN	41	0.10	4	0.08	0.00 <p< 0.22	
excavated	BLACK OAK	32	0.08	5	0.08	0.00 <p< 0.22	
cavities	BUCKEYE	8	0.02	0	0.04	0.00 <p< 0.14	
PLAIN	BLUE OAK	841	0.38	56	0.33	0.24 <p< 0.42	
TITMOUSE	WHITE OAK	272	0.12	30	0.17	0.10 <p< 0.24	
NESTS-	EVERGREEN	488	0.22	48	0.28	0.19 <p< 0.37	
natural	BLACK OAK	168	0.08	34	0.20	0.12 <p< 0.28	greater
cavities	BUCKEYE	438	0.20	2	0.01	0.00 <p< 0.03	lesser
WHITE-BR.	BLUE OAK	841	0.38	21	0.51	0.20 <p< 0.71	
NUTHATCH	WHITE OAK	272	0.12	8	0.19	0.03 <p< 0.34	
NESTS-	EVERGREEN	488	0.22	6	0.15	0.01 <p< 0.29	
natural	BLACK OAK	168	0.08	6	0.15	0.01 <p< 0.29	
cavities	BUCKEYE	438	0.20	0	0.00	---- ----	

[a] Species composition of plant groups: BLUE OAK = *Quercus douglassii*; WHITE OAK = *Q. garryana* and *Q. lobata*; EVERGREEN = *Q. wislizenii*, *Q. agrifolia*, *Q. chrysolepis*, *Umbellulalria californica*, and *Arbutus menzesii*; BLACK OAK = *Q. kellogi* and *Q. morehus* (Oracle oak); BUCKEYE = *Aesculus californicus*.
[b] Bonferoni confidence intervals (Neu et al. 1974);
[c] see Appendix C.