

# Potential Effects of Sudden Oak Death on Birds in Coastal Oak Woodlands<sup>1</sup>

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## Abstract

Tree pathogens can affect community composition and structure over wide areas. *Phytophthora ramorum*, cause of sudden oak death (SOD), occurs in the wild in California from Humboldt County to southernmost Monterey County. *P. ramorum* has killed many trees at some sites and may spread to affect near and distant forests. The pathogen has not yet been detected in San Luis Obispo County outside of nurseries, but threatens coast live oak (*Quercus agrifolia*) woodlands there. SOD-induced changes in vegetation structure and tree community composition may cascade to affect vertebrate communities. From 2002-2004 we counted breeding birds and measured habitat characteristics at 78 points distributed among four sites in coastal oak woodlands at high risk from SOD in San Luis Obispo County. Each point was visited three times each year to conduct 10-minute counts of all adult birds detected within 50 m. In 2004 we surveyed trees within 10 m of each point. We found 13 tree species; 63.8 percent of the individuals recorded were coast live oak and 19.6 percent were California bay laurel (*Umbellularia californica*). We recorded 75 bird species at the census points. The most abundant species were Steller's jay (*Cyanocitta stelleri*, 8.9 percent of individuals), orange-crowned warbler (*Vermivora celata*, 8.2 percent), dark-eyed junco (*Junco hyemalis*, 7.4 percent), and spotted towhee (*Pipilo maculatus*, 6.8 percent). Avian species diversity (Shannon-Wiener index) showed no clear pattern of variation with basal area of oaks (*Quercus* spp) and tanoaks (*Lithocarpus densiflorus*) in 2004 ( $r_s = -0.10$ ,  $0.2 < p < 0.5$ ), but oak titmouse (*Baeolophus inornatus*) abundance was associated with oak/tanoak basal area ( $r_s = 0.40$ ,  $p < 0.001$ ). We used these data to evaluate six habitat association models for cavity-nesting birds. Using  $QAIC_c$  as an information criterion, the most favorable model indicated that cavity-nesting birds select microsites with large-diameter trees (Akaike weight = 0.47). Changes in tree size class distribution resulting from SOD may lead to a slight decrease in cavity-nesting bird abundance over time. Effects on individual species may be more dramatic.

**Key words:** *Quercus agrifolia*, avian community structure, cavity-nesting birds, California Central Coast, disturbance, community dynamics

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## Introduction

Tree pathogens can act as keystone species, altering forest community composition and structure over wide areas (Hudler 1998). These changes may in turn affect faunal communities. Dutch elm disease (*Opiostoma ulmi*), for instance, has impacted avian populations in Europe and North America (Canterbury 1997, Osborne 1985, Osborne 1983, Osborne 1982). Haney and coworkers (2001) implicated chestnut blight (*Cryphonectria parasitica*) as one factor influencing historical changes in a southern Appalachian breeding bird community.

Sudden oak death (SOD), caused by the oomycete pathogen *Phytophthora ramorum*, causes high levels of adult tree infection and mortality (Brown and Allen-Diaz, this volume; Frankel and others, this volume; McPherson and others 2002, Garbelotto and others 2001). Although infection rates are generally higher for tanoak (*Lithocarpus densiflorus*) than for coast live oak (*Quercus agrifolia*) in the same stands (Swiecki and Bernhardt, this volume; McPherson and others 2002, Kelly and McPherson 2001), coast live oak mortality exceeds 50 percent of standing basal area at some locations in China Camp State Park in Marin County (Brown and Allen-Diaz, this volume).

*P. ramorum* has the potential to spread to near and distant regions and may dramatically affect vegetation structure in multiple forest communities (Cushman and Meentemeyer, this volume; Kelly and others, this volume; Oak and others, this volume; Meentemeyer and others 2004). SOD has not yet been detected in the wild in San Luis Obispo County, but threatens coast live oak woodlands there (Meentemeyer and others 2004). Coast live oak forests are highly susceptible to sudden oak death, in part because of high moisture levels in coastal areas. Rain is considered an important dispersal mechanism for *P. ramorum* spores (Davidson and others 2002). Also, California bay laurel (*Umbellularia californica*), which serves as a source of *P. ramorum* inoculum (Davidson and others 2002), is often an important overstory component of woodlands dominated by coast live oak. For these reasons, coastal forests in San Luis Obispo County may be at high risk of invasion by *P. ramorum*.

Over the short term, the death of a large proportion of the trees in a stand decreases canopy cover and may thus lead to an increase in shrub cover. As regeneration progresses, we may expect future stands to exhibit greater relative abundances of less susceptible tree species. California bay laurel, for instance, develops foliar lesions but does not suffer serious effects from *P. ramorum* (Davidson and others 2003) and thus may be more highly represented in future stands that have suffered high oak mortality.

Changes in vegetation structure and tree community composition resulting from sudden oak death may cascade to affect vertebrate communities and other ecosystem attributes (CalPIF 2002). The physical structure of vegetation is an important determinant of avian community composition; i.e., the species present and their relative abundances (e.g., Bub and others 2004, Urban and Smith 1989, Collins and others 1982, Anderson 1981).

The avifauna of coast live oak forests is relatively unstudied, although many of the breeding bird species in this system have been studied in other oak forest types (CalPIF 2002, Wilson and others 1991, Block 1989, Verner 1980). California oak woodlands are characterized by a high diversity of bird species (CalPIF 2002, Tietje and Vreeland 1997), many of which use acorns and cavities provided by mature oaks and tanoaks (Koenig 1990, Tietje 1990, Wilson and others 1991, Verner 1980). We would expect these vulnerable bird species, such as Acorn Woodpecker (*Melanerpes formicivorus*) and Oak Titmouse (*Baeolophus inornatus*), to become less abundant where oaks have declined in dominance (CalPIF 2002). Changes in canopy and shrub cover resulting from *P. ramorum* infestation would also be expected to change avian community composition. Dark-eyed Juncos (*Junco hyemalis*), for instance, are more abundant at sites with higher canopy cover (Tietje and Vreeland 1997, Tietje and others 1997). We would expect this species to be less abundant in an oak woodland infected with sudden oak death than at a comparable healthy site.

The objectives of this contribution are to (1) characterize the habitat structure and avifauna of coast live oak woodland in San Luis Obispo County, (2) describe how habitat structure affects the abundance of cavity-nesting birds, and (3) predict the potential effects of sudden oak death on cavity-nesting bird communities in high-risk coast live oak forests.

## **Study Area**

The coastal oak woodland landscape in San Luis Obispo County is a mountainous mosaic of woodland, pasture, chaparral, and ecotonal habitats, characterized by a high density of abrupt edges between habitat types (Vreeland and Tietje 2004). The overstory is dominated by coast live oak, with significant components of California bay laurel, Pacific madrone (*Arbutus menziesii*), and tanoak. Toyon (*Heteromeles arbutifolia*) is a common understory tree. The shrub layer is quite dense in places, and features such species as poison oak (*Toxicodendron diversiloba*), California blackberry (*Rubus ursinus*), and creeping snowberry (*Gaultheria hispidula*). Herbaceous ground flora include Western brackenfern (*Pteridium aquilinum*), California polypody (*Polypodium californicum*), fiesta flower (*Pholistoma* spp.), and

miner's lettuce (*Claytonia perfoliata*). Temperatures are moderated by the proximity of the ocean (Pavlik and others 1991), and do not reach the extreme highs and lows of more interior oak woodlands (Tempel and others, this volume). We examined climate data from National Oceanic and Atmospheric Administration weather stations (University of California 2005) from 1994 to 2004 and found that annual rainfall ranged from 276-939 mm at Morro Bay and 384-1052 mm at San Luis Obispo. Most of this precipitation falls during the winter months (November through April; Tempel and others, this volume). Winter rainfall is supplemented by fog interception (Pavlik and others 1991).

We surveyed breeding birds and measured habitat characteristics at four coastal oak woodland sites in San Luis Obispo County on the Central Coast of California, USA (fig. 1). The four sites include multiple ownerships and experience varied land uses. San Simeon Creek consists of two private residences and a portion of one private cattle ranch. Atascadero Ranches includes portions of two private cattle ranches. Camp San Luis Obispo consists of two areas within a National Guard base (Camp San Luis Obispo), used infrequently for training exercises and cattle grazing. Irish Hills consists of a rugged nature preserve owned by The Nature Conservancy, mostly inaccessible to human use.

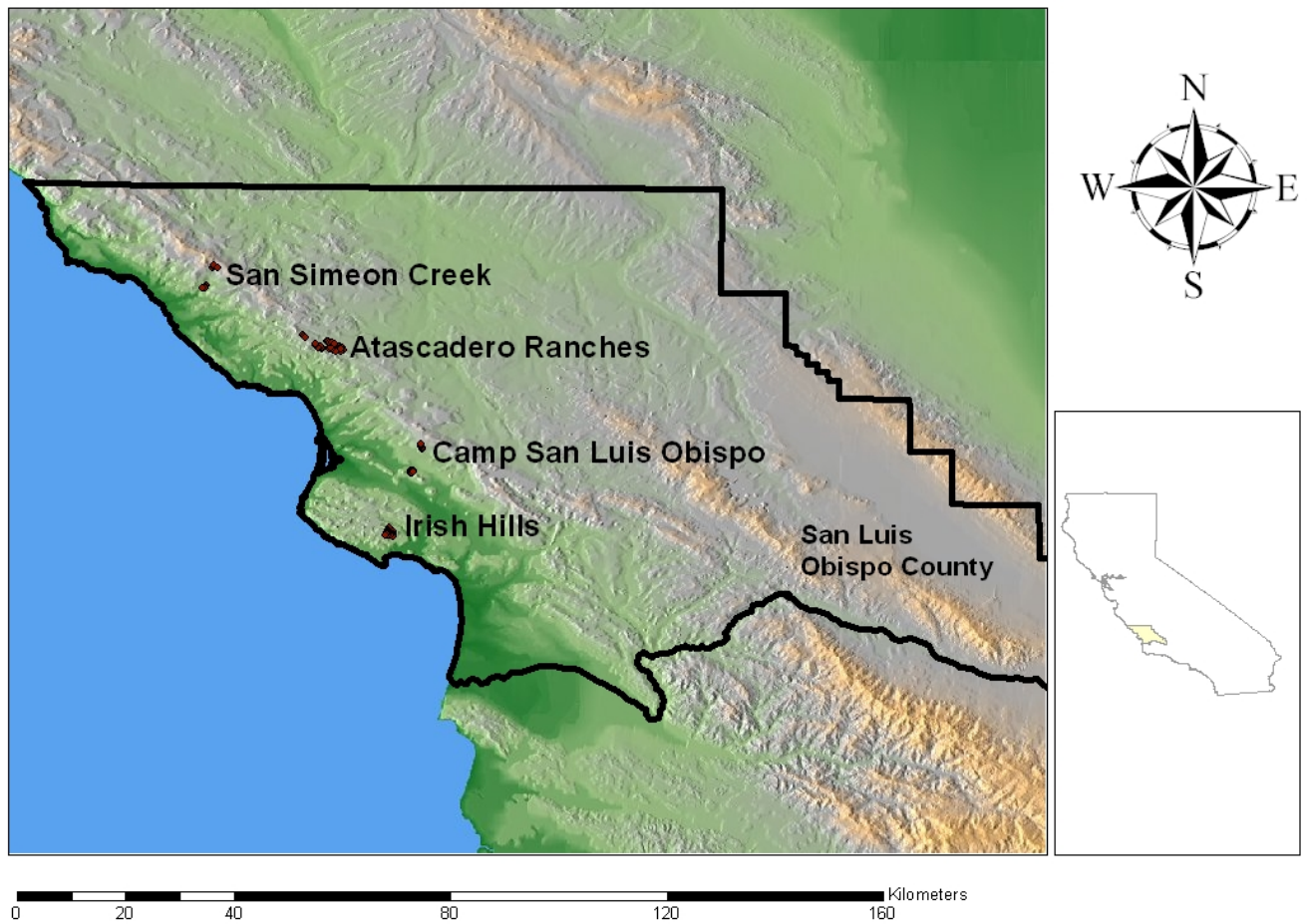
## Methods

### *Field methods*

We conducted 10-minute variable-radius counts (Ralph and others 1995) of breeding birds at 78 points distributed among the four sites from 2002-2004. This sample size is adequate for most purposes (Ralph and others 1995). Because our analyses involved predictors that vary among points and we modeled the abundance of a nesting guild (rather than individual species), we had plenty of statistical power to detect relationships. Count stations were located in coast live oak woodland and were  $\geq 250$  m apart. We visited each point at least three times from March to June of each year to conduct 10-minute variable-radius counts. One to three observers conducted counts in any given year. We rotated station visitations to balance observers, time of season, and time of day. All counts took place between sunrise and 1200 PDT. We recorded the species, sex (when known), and vocal behavior of each adult bird detected within the timed counts and estimated the distance of each bird from the observer. We censused 30 points at one site in 2002, 23 points at two sites in 2003, and 78 points at four sites in 2004.

We measured habitat characteristics within 25 m of each count point in 2004. We measured the diameter at breast height of each woody stem  $\geq 10$  cm within 10 m of

each count point. We recorded the species and status (dead or alive) of each stem and the number of cavities suitable for bird nesting on each one. A cavity was judged to be suitable for bird nesting if the opening was wide enough for an adult bird to enter. The four observers examined some stems together to reduce the subjectivity of these judgments.



**Figure 1**—Clouds of bird survey points at four sites in San Luis Obispo County.

We estimated canopy cover with densiometers at count points and 25 m in each cardinal direction. We measured shrub cover with a cover pole placed 25 m in each cardinal direction from each point. The pole was divided into five 0.5-m sections to measure visual obstruction from 0 to 2.5 m above the ground. Each section was subdivided into five 10-cm bands (alternating black and white). The observer stood 10 m from the pole in the direction of the point and recorded the number of bands in each section at least 25 percent obstructed by shrubs or other objects.

## ***Statistical analysis***

For each point where we surveyed birds in 2002 and 2003, we chose three visits in each year to correspond to the three visits in 2004. We matched these visits so that the dates sampled were similar among the three years. We determined the maximum number (among three visits) of individuals of each bird species detected within 50 m of each count point during the 10-minute surveys to obtain abundance indices for each species for each year. Using only data from 2004, we tallied the number of species detected at each point as an index of species richness and used the abundance estimates to calculate species diversity using the Shannon-Wiener index (Ricklefs 1979).

The distribution of cavity abundance among stems was not close to normal. Most stems had no cavities, but some had over 20. Rather than make distributional assumptions, we used a Spearman rank correlation test (SPSS 2003) to examine the association between tree diameter and number of cavities. We compared cavity counts on coast live oaks and bay laurels using a Mann-Whitney *U* test (SPSS 2003).

Using the tree survey data we calculated six habitat measures related to stand structure for each point station: total basal area, basal area of oaks and tanoaks, density of oak and tanoak stems, mean diameter at breast height, snag density, and cavity density. Avian species richness, as a count variable, would not be expected to be normally distributed. The Shannon-Wiener index can never be positive, so an assumption of normality does not seem appropriate for this index. Rather than make distributional assumptions, we used Spearman rank correlation tests (Zar 1996) to determine if avian species richness or diversity were related to the basal area of oaks and tanoaks in 2004.

We estimated canopy cover for each count area by averaging the five cover values measured in each plot. For shrub cover we calculated the percentage of bands at least 25 percent obstructed in the top four sections of the pole, because the bottom section was often obstructed by the ground or leaf litter. We then averaged the four shrub cover values for each plot.

For this contribution, we decided to model the abundance of birds in the cavity-nesting guild. By modeling an entire guild of species, rather than individual species, we hoped to uncover relationships useful for the conservation of multiple species (Block and others 1986). We calculated abundance of cavity-nesting birds by summing abundance indices for each species at each point. We reviewed species accounts in the California Wildlife Habitat Relationships (California Department of Fish and Game 2002) database in order to select appropriate habitat measures to include in candidate models. We developed a set of *a priori* poisson regression

models with cavity-nester abundance as the dependent variable, one or more habitat measures as predictor variables, temporal measures as “nuisance” predictors, and study site as a random effect. We considered observations from separate years to be repeated measures at the same points. We fitted these models with the GLIMMIX macro in SAS Proc Mixed (Littell and others 1996). We evaluated competing models for explanatory power and parsimony using a quasi-likelihood-based version of Akaike's Information Criterion ( $QAIC_c$ , Burnham and Anderson 2002).

We evaluated six competing models of cavity-nester abundance, using a poisson error structure with an overdispersion factor and site as a random effect. Predictor variables included five temporal nuisance parameters (year, earliest date of three visits, latest date of three visits, earliest start time of three visits, and latest start time of three visits) and the habitat measures relevant to each hypothesis. The candidate models included a cavity-availability limitation hypothesis (with cavity density as a habitat predictor), a snag-availability limitation model (with snag density), an acorn-availability limitation model (with oak/tanoak basal area), a multiple-limiting-factor hypothesis (with cavity density, snag density, and oak/tanoak basal area), a habitat selection hypothesis assuming a preference for oaks (with oak/tanoak basal area and density of oak/tanoak stems), and a habitat selection hypothesis assuming a preference for large-diameter trees (with mean diameter and total basal area).

We fitted the global model (including all considered nuisance and habitat measures) with various covariance structures and used  $QAIC_c$  to select the most appropriate one. The most favorable covariance structure was first-order autoregressive, so we used this structure with all subsequently fitted models. We then fitted a set of models that included all the habitat predictors, but varied by which nuisance parameters were included and whether site was included as a random effect. We compared all combinations in this model set and found the most favorable model to be the one including only year, latest date, and latest time (without site as a random effect).

We used available information on effects of sudden oak death on coastal oak woodland stand structure (Swiecki and Bernhardt, this volume; 2004; 2003) to simulate expected changes in an infected stand over 40 years. We used this simulation of habitat change to examine how cavity-nesting bird abundance might change under the selected habitat association model.

## Results

### ***Vegetation Attributes***

We found 13 tree species within 10 m of the count points; 42.2 percent of the stems recorded were coast live oak (*table 1*). The next most abundant species was California bay laurel, comprising 19.6 percent of the stems. Cavities were most abundant on old oak trees (*table 1, fig. 2*). Across species, cavity count increased with increasing diameter ( $r_s = 0.415$ ,  $p < 0.0005$ ,  $N = 1226$ , *fig. 2*). Coast live oak stems contained nearly four times as many cavities as California bay (*table 1, fig. 2*, Mann-Whitney  $U = 4794.5$ ,  $p < 0.0005$ ). Of 454 cavities on 1127 stems, only 11 were excavated by birds. Most cavities resulted from the scars of fallen limbs or decomposition of dead wood. Descriptive statistics for habitat measures are presented in *table 2*.

### ***Bird Community Structure***

We recorded 84 bird species at census points from 2002-2004, including 18 cavity-nesters, 15 species that use acorns, and five California endemics (CalPIF 2002). The overall 2004 Shannon-Wiener index was 3.5 (71 species, 1564 individuals). Of 75 species recorded within 50 m during the three years, the four most abundant species were all open-nesters: Steller's jay (*Cyanocitta stelleri*), orange-crowned warbler (*Vermivora celata*), dark-eyed junco (*Junco hyemalis*), and spotted towhee (*Pipilo maculatus*, *table 3*). Sixteen of these 75 species nest primarily in cavities.

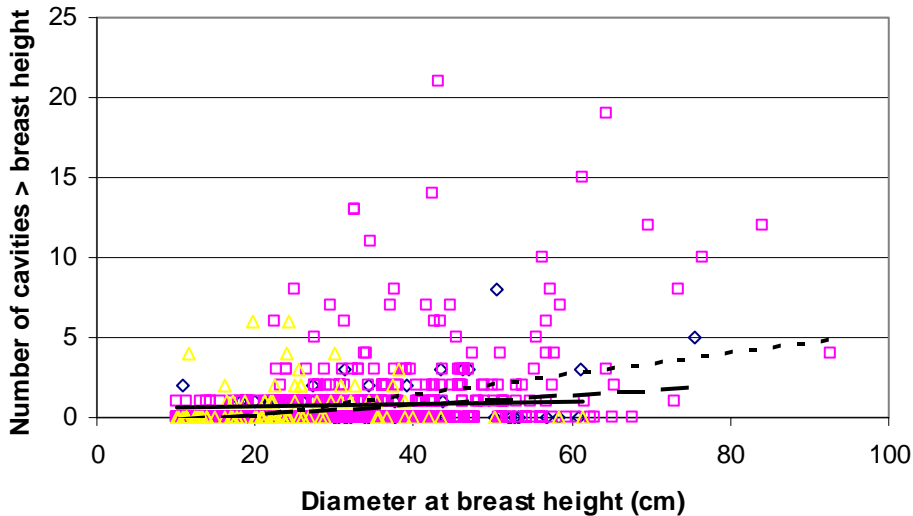
The basal area of oaks and tanoaks showed no clear relationship to species richness ( $r_s = -0.08$ ,  $0.2 < p < 0.5$ ) or diversity ( $r_s = -0.10$ ,  $0.2 < p < 0.5$ ) in 2004 (*fig. 3*). Counts of oak titmice were positively correlated with the basal area of oaks and tanoaks in 2004 ( $r_s = 0.40$ ,  $p < 0.001$ , *fig. 4*).



**Table 1**—Tree stems >10 cm diameter at breast height found in 78 plots of 10-m radius, centered at bird census points.

Species	Stems	Total cavities	Mean cavities/stem	Minimum # of cavities	Maximum # of cavities
California bay laurel ( <i>Umbellularia californica</i> )	82	48	0.59	0	8
Big-leafed Maple ( <i>Acer macrophyllum</i> )	11	3	0.27	0	1
California black oak ( <i>Quercus kelloggii</i> )	1	2	2.00	2	2
Ceanothus ( <i>Ceanothus</i> spp.) <sup>1</sup>	18	0	0.00	0	0
Coast live oak ( <i>Quercus agrifolia</i> )	177	398	2.25	0	21
Elderberry ( <i>Sambucus nigra</i> ssp. <i>caerulea</i> )	1	0	0.00	0	0
Gray pine ( <i>Pinus sabiniana</i> )	1	0	0.00	0	0
Pacific madrone ( <i>Arbutus menziesii</i> )	57	58	1.02	0	6
Tanoak ( <i>Lithocarpus densiflorus</i> )	31	0	0.00	0	0
Toyon ( <i>Heteromeles arbutifolia</i> )	26	2	0.08	0	2
Valley oak ( <i>Quercus lobata</i> )	8	10	1.25	0	6
Willow ( <i>Salix</i> spp.)	6	0	0.00	0	0
Total	419	521	1.24	0	21

<sup>1</sup>We found at least two species in this genus, but not all individuals were identified to species.



**Figure 2**—Relationship between diameter and the number of cavities for three most common tree species: coast live oak (squares), California bay laurel (diamonds), and Pacific madrone (triangles). Linear regressions of cavity count on diameter are indicated for oak (dotted line), bay (dashed line), and madrone (solid line).

**Table 2**—Descriptive statistics for habitat measures at 78 plots of 10 m radius, centered at bird census points.

Habitat Measure	Mean	Standard Error	Minimum <sup>1</sup>	Maximum
Mean diameter at breast height (cm)	26.42	0.89	0 <sup>2</sup>	55.50
Cavities per ha	2652.58	497.53	0	24191.55
Oak/tanoak stems per ha	332.59	28.12	0	1209.58
Oak/tanoak basal area (m <sup>2</sup> /ha)	24.55	1.79	0	66.45
Total basal area (m <sup>2</sup> /ha)	32.22	1.90	0	84.08
Snags per ha	37.14	5.52	0	190.99
% Canopy cover	81.63	1.68	23	98
% Shrub cover	54.63	2.32	7.50	96.25

<sup>1</sup>One plot contained no stems > 10 cm; thus minimum values for tree-stem variables are equal to zero.

<sup>2</sup>The value for the plot with no stems > 10 cm would technically be undefined, but we set this datum equal to zero to reflect that this plot contained only small trees.

### ***Habitat relationships of cavity-nesting birds and potential effects of SOD***

We fitted one model for each of the competing hypotheses of cavity-nester abundance (see Methods), only including the selected nuisance variables. The most favorable model was the large-diameter tree hypothesis (Akaike weight = 0.47, *table 4*). The large-diameter tree model fit the data adequately with the estimated overdispersion parameter (scaled deviance = 118.5,  $df = 130$ ,  $0.5 < p < 0.75$ ), but the range of observed values was substantially larger than the range of predicted values (*fig. 5*).

The habitat variables included in the large-diameter tree model include total basal area and mean diameter of all species. Sudden oak death would be expected to cause values of both of these habitat measures to decline (for information on the effect of diameter on susceptibility to sudden oak death see Swiecki and Bernhardt 2003, 2002a, 2002b). The parameter estimate for the effect of mean diameter on cavity-nester abundance was significantly greater than 0 (0.021, SE = 0.0082,  $t = 2.54$ ,  $df = 75$ ,  $p = 0.0132$ ), but the parameter estimate for the effect of basal area was not significantly different from 0 (-0.0011, SE = 0.00040,  $t = -0.29$ ,  $p = 0.7746$ , *table 5*).

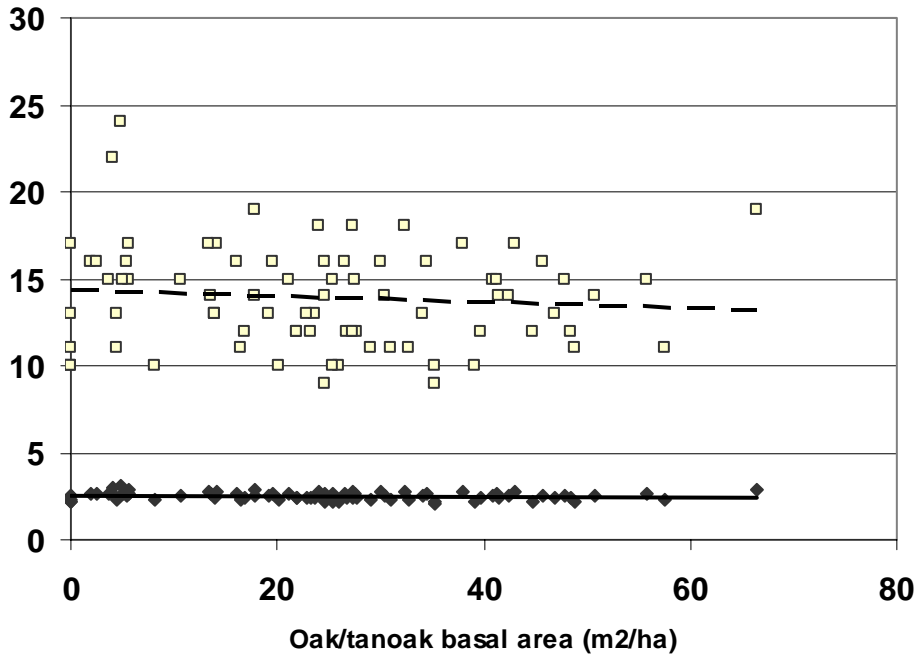
**Table 3**—Bird species detected within 50 m of 78 survey points during timed counts in 2002-2004. Only the 40 most abundant species are listed.

Species	Nesting Guild <sup>1</sup>	Birds per point <sup>2</sup>	Birds per ha (SE) <sup>3</sup>
Steller's Jay ( <i>Cyanocitta stelleri</i> )	canopy	1.69	2.16 (0.15)
Orange-crowned Warbler ( <i>Vermivora celata</i> )	ground	1.56	1.99 (0.13)
Spotted Towhee ( <i>Pipilo maculatus</i> )	ground	1.31	1.66 (0.11)
Dark-eyed Junco ( <i>Junco hyemalis</i> )	ground	1.42	1.81 (0.11)
Chestnut-backed Chickadee ( <i>Poecile rufescens</i> )	cavity	1.22	1.56 (0.18)
Pacific-slope Flycatcher ( <i>Empidonax difficilis</i> )	ground	0.98	1.25 (0.09)
Hutton's Vireo ( <i>Vireo huttoni</i> )	canopy	0.89	1.13 (0.07)
Warbling Vireo ( <i>Vireo gilvus</i> )	canopy	0.80	1.02 (0.12)
Oak Titmouse ( <i>Baeolophus inornatus</i> )	cavity	0.56	0.72 (0.10)
Bushtit ( <i>Psaltriparus minimus</i> )	canopy	0.50	0.64 (0.12)
House Wren ( <i>Troglodytes aedon</i> )	cavity	0.54	0.69 (0.09)
Black-headed Grosbeak ( <i>Pheucticus melanocephalus</i> )	canopy	0.50	0.63 (0.09)
Anna's Hummingbird ( <i>Calypte anna</i> )	canopy	0.37	0.48 (0.08)
Hairy Woodpecker ( <i>Picoides villosus</i> )	cavity	0.33	0.42 (0.06)
Northern Flicker ( <i>Colaptes auratus</i> )	cavity	0.29	0.37 (0.06)
Western Scrub-jay ( <i>Aphelocoma californica</i> )	canopy	0.33	0.42 (0.07)
Brown Creeper ( <i>Certhia americana</i> )	under bark	0.44	0.56 (0.06)
Bewick's Wren ( <i>Thryomanes bewickii</i> )	cavity	0.37	0.48 (0.07)
Wrentit ( <i>Chamaea fasciata</i> )	shrub	0.37	0.48 (0.07)
Purple Finch ( <i>Carpodacus purpureus</i> )	canopy	0.42	0.53 (0.06)
Lesser Goldfinch ( <i>Carduelis psaltria</i> )	canopy	0.38	0.49 (0.07)
Turkey Vulture ( <i>Cathartes aura</i> )	cliff	0.11	0.15 (0.04)
California Quail ( <i>Callipepla californica</i> )	ground	0.15	0.18 (0.05)
Mourning Dove ( <i>Zenaidura macroura</i> )	canopy	0.19	0.24 (0.05)
Band-tailed Pigeon ( <i>Columba fasciata</i> )	canopy	0.11	0.15 (0.04)
Acorn Woodpecker ( <i>Melanerpes formicivorus</i> )	cavity	0.12	0.16 (0.04)
Nuttall's Woodpecker ( <i>Picoides nuttallii</i> )	cavity	0.25	0.32 (0.05)
Cassin's Vireo ( <i>Vireo cassinii</i> )	canopy	0.14	0.17 (0.05)
American Crow ( <i>Corvus brachyrhynchos</i> )	canopy	0.15	0.18 (0.05)
Violet-green Swallow ( <i>Tachycineta thalassina</i> )	cavity	0.15	0.19 (0.05)
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	canopy	0.14	0.17 (0.04)
American Robin ( <i>Turdus migratorius</i> )	canopy	0.27	0.35 (0.06)
Townsend's Warbler ( <i>Dendroica townsendi</i> )	canopy	0.24	0.30 (0.06)
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	ground	0.26	0.33 (0.05)
Western Tanager ( <i>Piranga ludoviciana</i> )	canopy	0.11	0.15 (0.04)
California Towhee ( <i>Pipilo crissalis</i> )	shrub	0.17	0.21 (0.04)
Brewer's Blackbird ( <i>Euphagus cyanocephalus</i> )	canopy	0.11	0.14 (0.09)
American Goldfinch ( <i>Carduelis tristis</i> )	shrub	0.10	0.13 (0.04)
Ash-throated Flycatcher ( <i>Myiarchus cinerascens</i> )	cavity	0.08	0.11 (0.03)
Swainson's Thrush ( <i>Catharus ustulatus</i> )	shrub	0.08	0.11 (0.04)

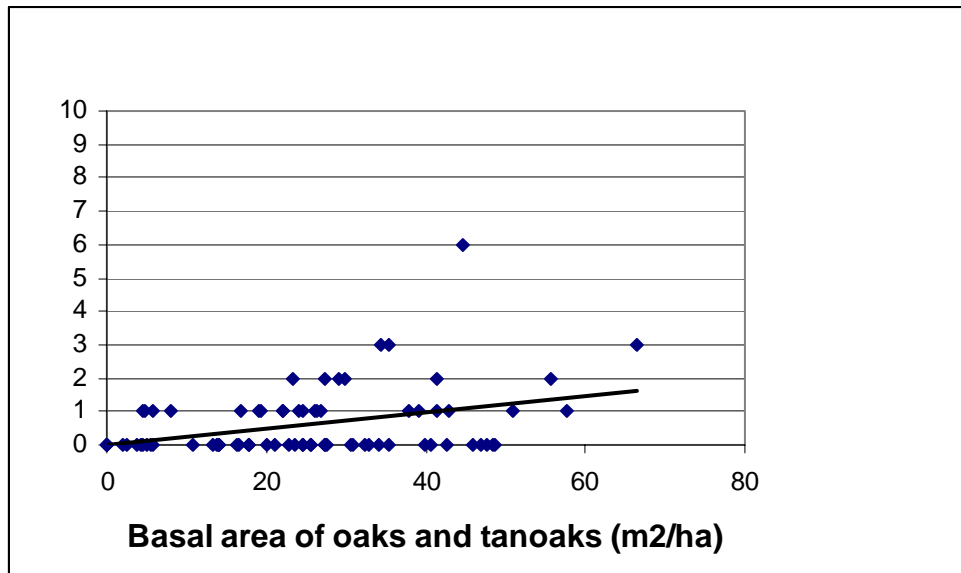
<sup>1</sup> Most frequent nest location for each species (Ehrlich and others 1988, Small 1994, personal observation).

<sup>2</sup> Sample size = 131 (30 points censused in 2002, 23 in 2003, and 78 in 2004).

<sup>3</sup> Estimated by dividing birds/plot by area within 50 m of plot center. These must be considered minimum estimates of density, because some individuals remain undetected (Buckland and others 1993).



**Figure 3**—Avian species richness (clear squares) and species diversity (Shannon-Wiener index, solid diamonds) in 2004 at 78 bird survey points varying in the basal area of oaks and tanoaks. Linear regressions of richness (dashed line) and diversity (solid line) on basal area are indicated.



**Figure 4**—Abundance of Oak Titmice (individuals per survey point) in 2004 at 78 bird survey points varying in the basal area of oaks and tanoaks. Linear regression of titmouse abundance on basal area is indicated.

**Table 4**—Model selection statistics for cavity-nesting bird abundance. The most favorable model (boldface font) indicates a habitat preference for stands with large-diameter trees.

Model	Scaled Deviance <sup>1</sup>	df	p	Over-dispersion	-2logL	Parameters	QAIC <sub>c</sub> <sup>2</sup>	Δi	w <sub>i</sub>
Cavity limitation	116.7	125	0.5<p<0.75	1.5739	244.8	8	184.2	3.0	0.105
Snag limitation	117.0	125	0.5<p<0.75	1.5980	245.1	8	184.4	3.2	0.095
Acorn limitation	116.7	125	0.5<p<0.75	1.5547	243.1	8	183.1	1.8	0.188
Multiple limiting factors	116.1	123	0.5<p<0.75	1.5526	243.4	10	187.9	6.7	0.017
<b>Large tree selection</b>	<b>118.5</b>	<b>124</b>	<b>0.5&lt;p&lt;0.75</b>	<b>1.4759</b>	<b>237.1</b>	<b>9</b>	<b>181.2</b>	<b>0.0</b>	<b>0.471</b>
Oak selection	116.9	124	0.5<p<0.75	1.5239	241.0	9	183.9	2.7	0.121

<sup>1</sup> Deviance (scaled by overdispersion factor) is used as a lack-of-fit statistic with df degrees of freedom; p is the probability of a fit as bad or worse as the observed deviance if the model is correct (Littell and others 1996).

<sup>2</sup> QAIC<sub>c</sub> is calculated from -2\*log-likelihood, the number of parameters in the model, and the sample size (131). The model with the lowest value of QAIC<sub>c</sub> is considered the most favorable model (Burnham and Anderson 2002). The QAIC<sub>c</sub> difference (Δi) for the most favorable model is by definition 0, and that model has the highest Akaike weight (w<sub>i</sub>).

We carried out a crude simulation of change in stand structure and cavity-nester abundance over 39 years in a SOD-affected coast live oak woodland, using vegetation parameters estimated from information published by Phytosphere Research (Swiecki and Bernhardt, this volume; 2004; 2003) and from our own habitat measurements (table 6).

Because the trees studied by Swiecki and Bernhardt (this volume, 2004, 2003) were greater in diameter than the mean diameter in our study plots, we estimated initial stem density at the Phytosphere plots by applying a regression equation of stem density on mean diameter from 77 of our study plots (stem density = 807.065 stems/ha – 11.217\*diameter in cm,  $t = -2.95$ ,  $p = 0.004$ , adjusted  $r^2 = 0.092$ , SPSS 2003) to the mean diameter reported by Swiecki and Bernhardt (2003). Every three years of the simulation we reduced the stem density based on the infection and failure parameters in table 6. We assumed the mean diameter of failed stems to be 48.5 cm, as reported by Swiecki and Bernhardt (2003), and used this value to calculate the mean diameter of remaining stems after each three-year increment. We assumed that recruitment exactly compensated for non-SOD mortality. We estimated basal area using the simplifying assumption that all trees were equal in diameter. After 39 years, 55.7 percent of the stems had failed, the basal area had declined from 47.2 to 14.8 m<sup>2</sup>/ha, and the mean diameter was 36.2 cm. Using these values of basal area and

diameter in the large-diameter model of cavity-nester abundance, we estimated a decline in cavity-nester abundance from 7.1 to 6.4 adults per ha over 39 years (fig. 6).

**Table 5**—Model statistics for large-diameter tree model of cavity-nesting bird abundance (individuals/point).

Effect	Numerator	Denominator	<i>F</i>	<i>p</i>	Parameter		
	<i>df</i>	<i>df</i>			Estimate	SE	<i>t</i>
Intercept		75		0.0065	1.247	0.445	2.8
Year	2	49	6.49	0.0032			
2002		49		0.0701	-0.377	0.203	-1.85
2003		49		0.0048	0.370	0.125	2.95
2004					0.000		
Latedate <sup>1</sup>	1	49	3.40	0.0712	-0.011	0.006	-1.84
Latetime <sup>2</sup>	1	49	2.06	0.1571	0.085	0.059	1.44
Meandbh <sup>3</sup>	1	75	6.44	0.0132	0.021	0.008	2.54
Totalba <sup>4</sup>	1	75	0.08	0.7746	-0.001	0.004	-0.29

<sup>1</sup>Latedate is the latest date of three visits in days after Vernal Equinox.

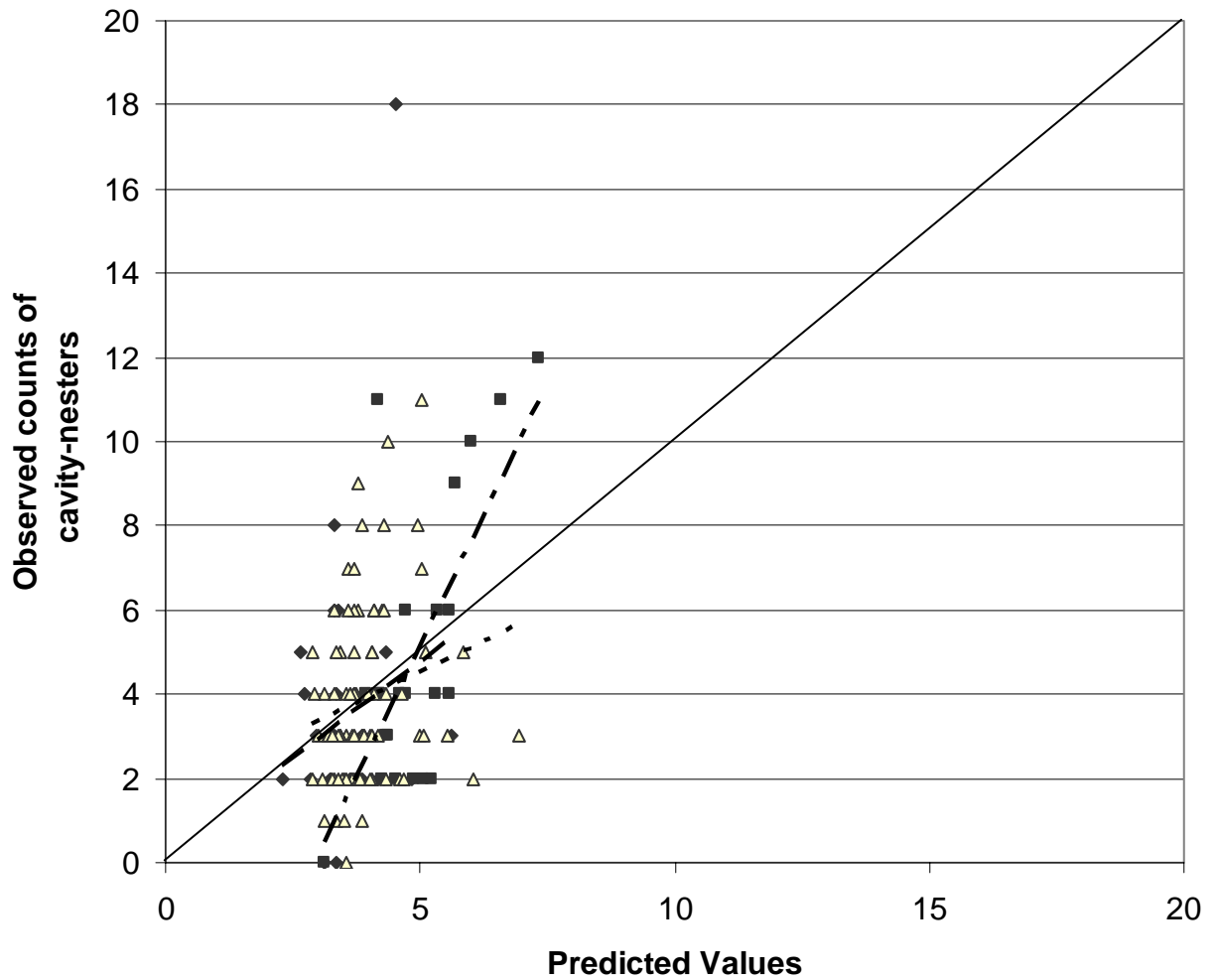
<sup>2</sup>Latetime is the latest start time of three visits in hours after sunrise.

<sup>3</sup>Meandbh is the mean diameter at breast height in cm of trees > 10 cm within 10 m of each survey point.

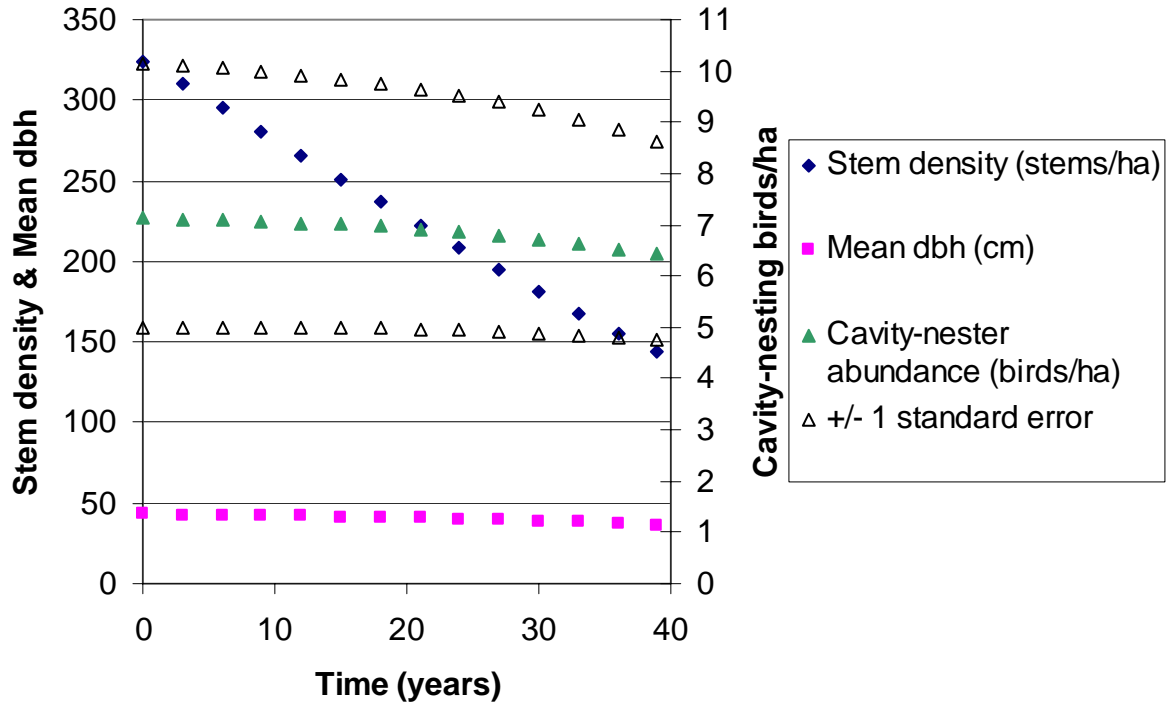
<sup>4</sup>Totalba is the total basal area in m<sup>2</sup>/ha of trees of all species > 10 cm diameter within 10 m of each survey point.

**Table 6**—Parameter values used in simulation of change in stand structure and cavity-nester abundance in response to sudden oak death.

Parameter	Symbol	Value	Units	Source
Initial proportion infected	$\iota$	0.224	Individual <sup>-1</sup>	Swiecki and Bernhardt (2004)
Rate of new infections	$\nu$	0.015	Individual <sup>-1</sup> *3 years <sup>-1</sup>	Swiecki and Bernhardt (2004)
Probability of failure with infection	$\varphi$	0.318	Individual <sup>-1</sup>	Swiecki and Bernhardt (2004)
Proportion of failures that are bole failures	$\beta$	0.58	Individual <sup>-1</sup>	Swiecki and Bernhardt (2004)
Bole failure rate	$\rho$	0.0028	Individual <sup>-1</sup> *3 years <sup>-1</sup>	$\nu*\varphi*\beta$
Mean diameter of failed stems	$\mu$	48.5	cm	Swiecki and Bernhardt (2003)
Mean diameter of non-failed stems	$o$	42.8	cm	Swiecki and Bernhardt (2003)
Initial mean diameter	$\delta$	43.1	cm	$\rho*\mu + (1 - \rho)*o$
Initial stem density	$\sigma$	324.1	stems/ha	See text.



**Figure 5**—Observed abundance of cavity-nesting birds from 2002-2004 at 78 bird survey points plotted versus values predicted from the large-diameter tree habitat preference model. Points from 2002 are indicated by diamonds, from 2003 by squares, and from 2004 by triangles. Solid line indicates hypothetical perfect prediction of observed values. Linear regressions of observed on predicted values are indicated (dashed line, 2002; alternating dots and dashes, 2003; dotted line, 2004).



**Figure 6**—Simulation of change in stand structure and cavity-nester abundance over 39 years in coast live oak woodland infected with sudden oak death. Minimal standard errors of cavity-nester abundance were estimated by substituting values of mean-dbh coefficient adjusted by +/- 1 SE (*table 5*). Error estimates would be greater if SE's of other parameter estimates were considered.

## Discussion

Although researchers have devoted considerable effort toward modeling habitat relations of birds in California oak woodlands (e.g., Wilson and others 1991, Block 1989, Dedon and others 1986), woodlands dominated by coast live oak deserve more attention. Bird species often vary geographically in habitat relations (Block and Morrison 1991), and avian communities vary in the relative abundances of species in common. For instance, we found that the most abundant bird species were open-nesting birds, while blue oak (*Quercus douglasii*) woodlands are often dominated by cavity-nesters (Wilson and others 1991). Tempel and others (this volume) found the most abundant breeding bird species in blue oak woodlands in San Luis Obispo



County to be the cavity-nesting Oak Titmouse, although open-nesters were well-represented among the most common species.

The high diversity of breeding birds we observed in coast live oak woodlands demonstrates the rich biota characteristic of this habitat. In contrast, Wilson and others (1991) found 51 breeding bird species in blue oak woodland near Hopland, California. Tempel and others (this volume), however, found higher avian species diversity (Shannon-Wiener index) and richness in blue oak woodlands at Camp Roberts than at our coastal oak woodland sites.

Of the models we examined, the most favorable in terms of fit and parsimony indicated that cavity-nesters prefer stands with large trees. The limiting-factor models were inferior to this habitat selection model when all three years of avian census data were considered. Model selection on 2004 data alone, however, indicated that limiting factors such as cavity and acorn availability may be important. Although secondary cavity-nesting birds are often assumed to be limited by nest-site availability, this is not always true in California oak woodland habitats (Waters and others 1990). Excavating species, such as woodpeckers, might be expected to be limited by the availability of snags. Snag availability was not an important factor in determining cavity-nester abundance in any of the models we examined. Because large living oaks tend to have many cavities (*table 1, fig. 2*) and dead branches suitable for excavation (Garrison and others 2002), snag availability is not likely to be limiting for cavity-nesting birds in California oak woodlands. Acorn woodpeckers along the Pacific coast may be limited by acorn abundance and diversity (Koenig and Haydock 1999), but it seems unlikely that an entire nesting guild would be limited by this food resource.

In highly mobile organisms such as birds, we might expect local abundances to be determined by habitat preference rather than by limiting resources. It is important to remember that preferred habitats are not necessarily optimal habitats in terms of individual fitness or population viability (Battin 2004, Purcell and Verner 1998). Modeling relationships between abundance of animals and habitat characteristics is only the first step in understanding how populations may change with habitat alteration. Information on breeding success, mortality, and dispersal is necessary for demographic modeling.

The simulation of change in stand characteristics with *P. ramorum* infection indicated that cavity-nester abundance might only experience slight declines even with dramatic overstory mortality. This is not a surprising result, given that cavity-nesting birds are common in open oak woodlands. There are reasons to be skeptical of these results, however. The selected model of cavity-nester abundance has not

been validated on other data sets, and thus we cannot know if it is generalizable to coastal oak woodland birds at other sites (Morrison and others 1992). It might not even be generalizable to the sites we studied, considering that we observed variation in apparent habitat relations among years. Furthermore, we have not yet conducted sensitivity analyses, and simulation results are likely to be sensitive to initial parameters. Values and variance of parameters can be refined as specific information on the effects of sudden oak death on vegetation structure becomes available (Brown and Allen-Diaz, this volume).

How can we build better models? We fitted a *post hoc* model with observer history as an additional nuisance variable. The results suggested that the marked overdispersion in 2002 was due to variation among observers, but the additional parameters made this model less favorable by  $QAIC_c$  than the previously selected model. Because bird species vary in habitat relations, the total abundance of cavity-nesters averages over counts of individual species that may increase or decrease with habitat predictors. For instance, secondary cavity nesters might be influenced by cavity availability, but excavators would not be dependent on this resource. We anticipate that tighter fits will be obtained when we model the abundances of individual species, given that species vary in habitat associations. This is suggested by the observation that counts of oak titmice were positively correlated with the basal area of oaks and tanoaks, but avian species richness and diversity (community attributes) were not related to oak/tanoak basal area. The simulation of change in vegetation structure in SOD-affected woodland could be much improved with species- and size-class-specific data on infection and mortality rates of trees from affected stands.

If sudden oak death becomes established in San Luis Obispo County, it could alter much of the remaining coast live oak woodland. As trees die and fall, the canopy would become more open, woody debris would accumulate on the ground, and increased light levels may result in dense shrub cover. We may expect that sudden oak death would lead to an increase in the representation of bay laurel in affected stands. This change in tree species composition might be detrimental to birds for several reasons. We found lower numbers of cavities on bay trees than on coast live oaks, so cavity-nesting birds may find fewer nest sites in SOD-affected stands. We might also expect bird species that use acorns to decline in number as the oaks become less dominant. In addition, Apigian and Allen-Diaz (this volume) found that oak titmice preferentially forage in the canopies of coast live oaks. Titmice and chestnut-backed chickadees (*Poecile rufescens*) avoid bays, which harbor fewer insect prey items.

Because many of these bird species vary in habitat relations over space and time (Block and Morrison 1991), care should be exercised in extending these findings to other oak woodland types. Long-term studies are needed in multiple habitats. Variation in climate among years can affect food availability and predation risk of songbirds (Sillet and others 2000, Morrison and Bolger 2002). Variation in acorn productivity among years (Koenig and others 1991) may also cause temporal variation in avian abundance. It is especially important for standardized censuses to be conducted in woodlands experiencing structural changes, such as those affected by sudden oak death.

### **Recommendations for management**

We should make every effort to insure that *P. ramorum* does not become established in San Luis Obispo County or otherwise expand beyond its current range. Current regulations for survey and control of nursery and agricultural industries should be followed with diligence and resolve. Given the possibility that human recreationists may be important vectors for the pathogen (Cushman and Meentemeyer, this volume), it would be valuable to develop infrastructure to help hikers and bikers clean equipment and vehicles before leaving infected areas (Thut and others, this volume). Inaccessible forests such as the nature preserve in the Irish Hills may prove to be valuable refugia for coast live oaks.

Forest and rangeland managers should retain large oaks with numerous cavities to provide foraging and nesting sites for cavity-nesting birds. Diseased and dead oaks should only be removed from infected stands if it can be confidently established that so doing will contain the infestation.

### **Conclusions**

Sudden oak death is likely to change stand structure in ways important to breeding birds. Cavity-nesting birds may be affected by changes in the size class distribution of trees or the availability of cavities and acorns. Nevertheless, sudden oak death is unlikely to have dramatic effects on the abundance of cavity-nesters as a guild in the short term. Effects on individual species may be more dramatic.

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