

Vegetation and Small Vertebrates of Oak Woodlands at Low and High Risk for Sudden Oak Death in San Luis Obispo County, California¹

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Abstract

San Luis Obispo County contains oak woodlands at varying levels of risk of sudden oak death (SOD), caused by a fungal pathogen (*Phytophthora ramorum*) that in the past decade has killed thousands of oak (*Quercus* spp.) and tanoak (*Lithocarpus densiflorus*) trees in California. SOD was most recently detected 16 km north of the San Luis Obispo County line. Low-risk woodlands occupy 57 percent of the county's land area, whereas high-risk woodlands occupy only 1 percent. During 2002-2004, we collected data on vegetative structure and small vertebrate (birds, small mammals, amphibians, reptiles) abundance in both types of woodland within the county. One study site was located in low-risk habitat and two in high-risk habitat. The two high-risk sites were similar in terms of vegetative structure and wildlife, while being much different from the low-risk site. Of the 11 vegetation attributes measured, tree density, basal area, canopy cover, coarse woody debris, and litter depth were greater at both high-risk sites ($P < 0.05$). Small mammals and amphibians were more abundant at the high-risk sites ($P < 0.05$), while birds and reptiles were more abundant at the low-risk site ($P < 0.05$). Species that were notably abundant in high-risk compared to low-risk habitat included the chestnut-backed chickadee (*Poecile rufescens*), Steller's jay (*Cyanocitta stelleri*), orange-crowned warbler (*Vermivora celata*), dusky-footed woodrat (*Neotoma fuscipes*), brush mouse (*Peromyscus boylii*), Monterey salamander (*Ensatina eschscholtzii eschscholtzii*), and slender salamander (*Batrachoseps* spp.). Due to the scarcity and fragmented distribution of high-risk woodlands within San Luis Obispo County, these wildlife species may be severely impacted if the pathogen reaches the county.

Key words: California, oak woodlands, *Phytophthora ramorum*, *Quercus agrifolia*, small vertebrates, sudden oak death, wildlife habitat

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Introduction

Many wildlife species utilize California's oak woodlands (*Quercus* spp.) for food, shelter, and reproduction (Pavlik and others 1991, California Department of Fish and Game 2002). Acorns are such an important food resource that deer and rodent populations can fluctuate in synchrony with the annual mast crop (Barrett 1980). Food resources are not limited to acorns, however. The dusky-footed woodrat (*Neotoma fuscipes*) feeds heavily upon coast live oak (*Quercus agrifolia*) shoots and leaves in some locations (Linsdale and Tevis 1951), and several bird species preferentially forage on oak trees (Block and Morrison 1987, Apigian and Allen-Diaz this volume). Some species, such as the acorn woodpecker (*Melanerpes formicivorus*), may even be dependent upon oaks for their continued survival (CalPIF 2002).

California oak woodlands are threatened, however, by natural and anthropogenic disturbances, including poor oak regeneration, firewood cutting, housing and vineyard development, and severe wildfires (Merenlender 2000, Fire and Resource Assessment Program 2003). Within the last 10 years, perhaps the most serious threat to emerge has been sudden oak death (SOD), a disease caused by the fungal pathogen *Phytophthora ramorum*. This pathogen primarily kills coast live oak, tan oak (*Lithocarpus densiflorus*), and California black oak (*Q. kelloggii*) (Rizzo and Garbelotto 2003). Although we currently have little knowledge of the disease's impacts upon wildlife communities, previous forest pathogen outbreaks suggest that significant impacts to wildlife may occur (Liebhold and others 1995).

In San Luis Obispo County, the Agriculture and Open Space Element of the General Plan makes mention of the scenic beauty and wildlife habitat provided by the county's coastal oak woodlands (San Luis Obispo County 1998), and a recent revision (San Luis Obispo County 2004) remarked: "... special standards need to be applied so that the woodlands are protected". Although SOD has not yet been identified in San Luis Obispo County, the disease is currently known in southern Monterey County, 16 km north of the San Luis Obispo County line. Meentemeyer and others (2004) identified 102 km² of San Luis Obispo County's coastal oak woodland (1.2 percent of the total county area) to be at high risk for the disease compared to 4,891 km² at low risk (56.9 percent of the total county area). Nearly all high-risk areas occur within 20 km of the coast in the northern third of the county and in a mosaic that is closely associated with medium- and low-risk habitats. If the disease becomes established in San Luis Obispo County, planners and natural resource managers will require information on the habitat and faunal characteristics of the high-risk coastal oak woodlands on which to base protective measures.

We sampled the habitat structure and wildlife communities in San Luis Obispo County oak woodlands at one site at low risk of SOD infection and two sites at high risk. We chose to study four wildlife taxa (birds, small mammals, amphibians, and reptiles), which we believed would be sensitive to habitat alterations caused by SOD should the disease become established in the county. Our study objectives were to: 1) compare vegetation attributes and small vertebrate occurrences and relative abundances in oak woodlands at low risk and high risk for SOD, and 2) provide baseline data on the habitat and small vertebrate wildlife potentially useful to natural resource planners and managers striving to protect the wildlife within the county's oak woodlands.

Study Areas

Low-Risk Habitat

Our low-risk (hereafter “LR”) study site was within the “high country” of Camp Roberts, a training facility of the Army National Guard in north-central San Luis Obispo County (*fig. 1*), at which we have conducted wildlife research since 1993. The northern portion of Camp Roberts is in Monterey County. Within the 17,800-ha facility, 7,200 ha are classified oak woodland (Camp Roberts 1989). The woodland is within the area classified by Meentemeyer and others (2004) at low risk of SOD infection. Blue oak (*Quercus douglasii*), a non-host of *P. ramorum*, is the predominant tree species in the overstory with a variable contribution of coast live oak. When present, the understory is composed of poison oak (*Toxicodendron diversilobum*), toyon (*Heteromeles arbutifolia*), redberry (*Rhamnus crocea*), bigberry manzanita (*Arctostaphylos glauca*), and ceanothus (*Ceanothus* spp.). On the woodland floor, wild oats (*Avena* spp.), bromes (*Bromus* spp.), and fescues (*Festuca* spp.) dominate. Common forbs include deerweed (*Lotus scoparius*), fiddleneck (*Amsinckia* spp.), filaree (*Erodium* spp.), hummingbird sage (*Salvia spathacea*), and the exotic yellow star thistle (*Centaurea solstitialis*). Most of the “high country” on Camp Roberts receives minimal use by military personnel and is not managed specifically for livestock, woodcutting, or other land-use activities. Sheep grazing is conducted on Camp Roberts each spring, but our study sites receive minimal or no grazing due to the steep terrain and dense shrub and tree cover.

High-Risk Habitat

In 2002, within areas of high risk (hereafter “HR”) habitat in San Luis Obispo County, we established two study sites (hereafter HR1 and HR2) on private cattle ranches (*fig. 1*). Sites were chosen based on accessibility and the presence of coast

live oak woodlands having large oak trees (>50 cm dbh), a dense canopy layer, and California bay (*Umbellularia californica*) as a co-dominant tree species. The presence of California bay is a strong predictor of woodlands at high risk for SOD (Meentemeyer and others 2004). Lesser amounts of Pacific madrone (*Arbutus menziesii*) and tanoak are present. The understory is composed of shrubs, including California blackberry (*Rubus ursinus*), creeping snowberry (*Gaultheria hispidula*), poison oak, and toyon. Ground vegetation comprises a mix of herbaceous plants such as Western bracken fern (*Pteridium aquilinum*), California polypody (*Polypodium californicum*), fiesta flower (*Pholistoma* spp.), and miner's lettuce (*Claytonia perfoliata*). Our study sites receive only minimal grazing by cattle due to the steep terrain and limited production of forage.

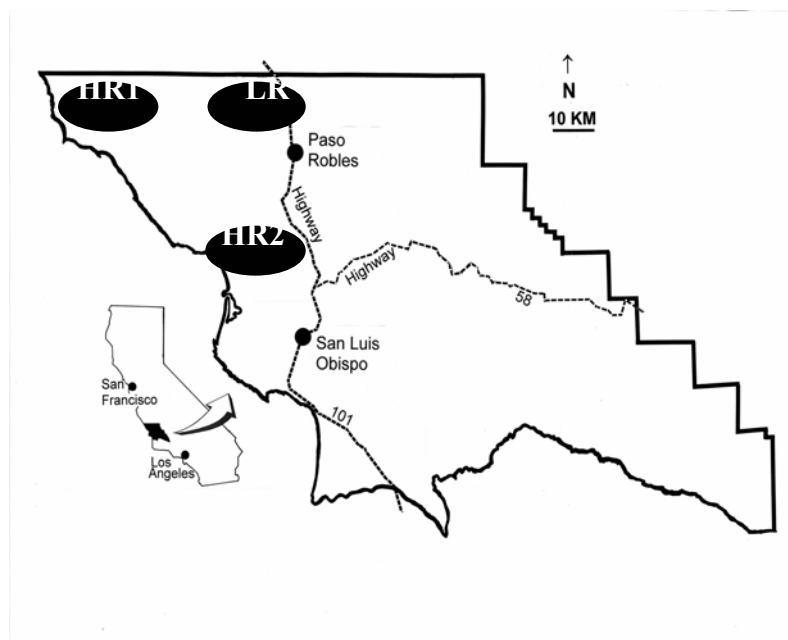


Figure 1—Location of study sites containing oak woodlands at low risk and high risk of SOD infection, San Luis Obispo County, California, 2002-2004. LR = low-risk site, HR1 = high-risk site 1, HR2 = high-risk site 2.

Methods

Field Methods

Vegetation

We gathered data on the following vegetation attributes: tree (≥ 10.0 cm dbh) density and diameter, snag (≥ 10.0 cm dbh) density and diameter, shrub cover, canopy cover, coarse woody debris (CWD) volume, litter depth, and number of woodrat dwellings (hereafter “houses”). At site LR, we primarily used vegetation data from prior studies. The sampling protocol for snags, canopy, shrubs, litter, and woodrat houses

is described in Vreeland and Tietje (2002). The sampling protocol for trees is described in Tietje and others (1997). In February 2005, we collected more detailed CWD data at site LR on 11 randomly selected small-mammal trapping grids (see below). Within each grid, we located four sampling plots at random grid intersections (44 plots total). From the plot center, we established 10-m transects in each cardinal direction and recorded the length and diameter of each CWD piece (≥ 7.6 cm in diameter, ≥ 1 m in length) crossing a transect (Waddell 2002). In 2004, we collected data on all of the above vegetation attributes on 10 small-mammal trapping grids (see below) on the HR sites (three at site HR1, seven at site HR2). Within each grid, we located eight plots at random grid intersections (80 plots total). We used the same plot design (10-m-radius circle) and sampling techniques used at site LR with the exception of tree density. Whereas we had used a point-center quarter method at site LR (Cottam and Curtis 1956), we opted to count all trees within each plot at sites HR1 and HR2.

Breeding Birds

At sites LR and HR2 during March-June, 2002-2003, we conducted point-counts of breeding birds at point-count stations that were at least 150 m apart. In 2002, we visited 86 point-count locations at site LR and 30 point-count locations at site HR2. In 2003, we visited a subset of 12 randomly selected point-count locations at each site. Each year, we made five visits to a sampled point-count location. Each visit lasted 10 minutes and occurred between official sunrise and 1100 hours. We recorded all birds detected within 50 m of a point per standard breeding-bird survey protocols (Bibby and others 1992).

Small Mammals

We sampled small mammals on 1.1-ha, 8 X 8 trapping grids (64 intersections, 15-m spacing). We trapped on 22 grids at site LR, three grids at site HR1, and five grids at site HR2 (adding two more grids at HR2 for the final trapping session and for sampling vegetation [see above]). We conducted trapping sessions during April-May 2003, October-November 2003, and April-May 2004. We trapped for three consecutive nights. We placed a single Sherman live trap (7.6 X 9.5 X 30.5 cm) baited with COB (rolled corn, oats, and barley laced with molasses) at each grid intersection. We tagged captured animals with individually numbered ear tags and recorded the tag number, species, capture location, sex, mass (g), and age class (juvenile or adult). If an individual's pelage was >25 percent gray, we recorded the animal as a juvenile. We handled the animals in accordance with the University of

California, Berkeley, Animal Use Protocol #R166-0199, and released them at the site of capture.

Amphibians and Reptiles

During 2002-2004, we counted amphibians and reptiles under plywood coverboards as described in Tietje and Vreeland (1997). At sites HR1 and HR2, we placed coverboards along the A, C, F, and H rows of 8 X 8 small mammal trapping grids, for a total of 32 coverboards per grid. (We did not place coverboards on the grids added to HR2 in 2004 for trapping small mammals and sampling vegetation [see above].) At site LR, we sampled coverboards along alternate rows of 17 X 17 trapping grids (17 X 8; 136 coverboards per grid) that we have used for wildlife study since 1993 (Tietje and others 1997). From January to mid-May, we checked each coverboard every 2-3 weeks. We recorded the location, species, and number of individuals for all detections. In 2002, we checked coverboards at site LR (eight grids) and site HR2 (five grids). In 2004, we checked coverboards at site HR1 (three grids) and site HR2 (five grids). We made eight sampling visits to each grid in 2002 and six visits to each grid in 2004. Three species of slender salamander (*Batrachoseps nigriventris*, *B. incognitas*, and *B. minor*) potentially occur at each study site (Jockusch and Wake 2002). These species cannot be distinguished in the field, so we grouped all *Batrachoseps* species into one category (hereafter “slender salamanders”).

Data Analysis

Climate

We downloaded climate data for San Luis Obispo County weather stations from an online database (University of California 2004). We used data from stations operated by the U.S. Department of Commerce/National Oceanic and Atmospheric Administration. We obtained daily maximum temperature, minimum temperature, and precipitation data from 1994-2004 for three weather stations near our study sites. We chose station #NCDC 6730 (Paso Robles) for its proximity to site LR, and stations #NCDC 5866 (Morro Bay) and #NCDC 7851 (San Luis Obispo) for their proximity to sites HR1 and HR2. We then calculated average daily values over the 10-year period for the “low-risk” weather station data and for the combined data of the “high-risk” stations.

Vegetation

We compared 11 vegetation attributes among study sites using a 1-way ANOVA ($\alpha = 0.05$; Quinn and Keough 2002). We treated each trapping grid as a sampling unit. Thus, each vegetation plot within a grid was a subsample. We calculated CWD volume according to Waddell (2002). We transformed CWD volume (natural log) and canopy cover (arcsine) to achieve normal distributions.

Breeding Birds

We used the California Wildlife Habitat Relationships computer program (California Fish and Game 2002) to identify breeding bird species in each habitat type. For each breeding bird species, we calculated its annual relative abundance at each point-count location by using the maximum number of individuals recorded during a single visit. We then computed an annual Shannon-Wiener diversity index at each point-count location using the species abundance data (Ricklefs 1979). We determined the annual species richness at each point-count location by counting the total number of breeding bird species recorded from all five visits. We compared attributes of the bird community (*see table 3*) between the two study sites using a 3-way ANOVA ($\alpha = 0.05$; Quinn and Keough 2002) with site, time period (year), and their interaction as the independent variables. We were mainly interested in study site as the independent variable, but included time and a time*site interaction term to control for temporal variation.

Small Mammals

For all small mammal species, we calculated seasonal relative abundance on each grid by determining the minimum number of animals (MNA) captured during each trapping session. We then computed the Shannon-Wiener diversity index for each trapping session on a grid using the species abundance data (Ricklefs 1979). We determined seasonal species richness on each grid by counting the total number of species recorded during each trapping session. Because small mammals frequently lost weight with successive captures during a trapping session, we used the maximum weight recorded for each individual during a trapping session. We compared attributes of the small mammal community (*see tables 4 and 5*) among study sites using a 3-way ANOVA ($\alpha = 0.05$; Quinn and Keough 2002) with site, time period (trapping session), and their interaction as the independent variables. We were mainly interested in study site as the independent variable, but included time and a time*site interaction term to control for temporal variation. Because sample sizes varied among study sites, we used Type III sum of squares to determine statistically significant

effects (Quinn and Keough 2002). When ANOVA indicated that study site was a significant factor for a given variable, we performed pairwise comparisons among study sites using Ryan's Q test (Quinn and Keough 2002).

Amphibians and Reptiles

We calculated the annual relative abundance of each amphibian and reptile species on each grid by using the maximum number of individuals recorded during a single visit. Because grids at site LR contained more coverboards than grids at sites HR1 and HR2 (136 vs. 32), we divided the species abundance on each LR grid by 4.25. For both the amphibian and reptile communities, we then computed an annual Shannon-Wiener diversity index on each grid using the species abundance data (Ricklefs 1979). We determined annual species richness on each grid by counting the total number of species recorded during all visits. We compared attributes of the amphibian and reptile communities between sites LR and HR2 (2002 data, see *table 6*) and between sites HR1 and HR2 (2004 data, see *table 7*). We were unable to transform either the amphibian or reptile abundance data to achieve a normal distribution, so we performed non-parametric Mann-Whitney U tests for each comparison ($\alpha = 0.05$; Quinn and Keough 2002).

Results

Climate

Temperature extremes at the Paso Robles weather station (in effect, "low-risk" habitat) were greater than those at the Morro Bay and San Luis Obispo weather stations (in effect, "high-risk" habitat, *table 1*). Although all weather stations experienced arid conditions during the warmer months (May-October), precipitation during the cooler months (November-April) averaged 20 cm more at the "high-risk" stations (*table 1*).

Table 1—Average daily maximum and minimum temperatures and seasonal precipitation at three weather stations near study sites containing oak woodlands at low risk (LR) and high risk (HR) of SOD infection, San Luis Obispo County, California, 1994-2004. Climatic data was obtained from weather stations operated by the U.S. Department of Commerce/National Oceanic and Atmospheric Administration. The LR weather station was at Paso Robles, California, and the HR weather stations were at Morro Bay and San Luis Obispo, California.

	LR	HR
Average daily temperatures (°C)		
Maximum (May-October)	30	22
Minimum (May-October)	9	11
Maximum (November-April)	18	18
Minimum (November-April)	3	7
Average seasonal rainfall (cm)		
May-October	3	5
November-April	32	52

Vegetation

At site LR, all trees were either blue oak (81 percent) or coast live oak (19 percent). In contrast, sites HR1 and HR2 contained greater amounts of coast live oak and a more diverse tree community. At these two sites, observed tree species included coast live oak (58 percent), California bay (24 percent), and madrone (12 percent). The remaining 6 percent of the trees were predominantly tanoak, valley oak (*Quercus lobata*), and bigleaf maple (*Acer macrophyllum*).

Both HR sites (HR1, HR2) had well-structured overstories, compared to site LR. Tree density was over twice as great and tree basal area over three times greater on both HR sites (*table 2*, $P < 0.05$). In addition, tree canopy covered approximately 90 percent of both HR sites, compared to 74 percent of site LR (*table 2*, $P < 0.05$). Presumably due to their greater tree densities, both HR sites also had more CWD and a deeper litter layer than site LR (*table 2*, $P < 0.05$).

Site LR did have higher observed values than either site HR1 or HR2 for some vegetation attributes. Due to a more open canopy, shrub cover was greater at site LR (*table 2*, $P < 0.05$). In addition, we observed a greater density of woodrat houses ($P < 0.10$) and snags ($P < 0.10$) at site LR, although the differences were not significant at our specified α level of 0.05.

Table 2— Mean values (and standard errors) of vegetation attributes on study sites containing oak woodlands at high risk (HR1, HR2) and low risk (LR) of SOD infection, San Luis Obispo County, California.

	HR1 (n = 3)	HR2 (n = 7)	LR (n = 11)*
Tree density (stems/ha)	^A 493.5 (201.3)	^A 506.0 (26.7)	^B 238.6 (22.9)
Tree diameter (cm)	^A 30.9 (5.4)	^{AB} 27.6 (0.7)	^B 22.6 (0.8)
Tree basal area (m ² /ha)	^A 29.5 (1.0)	^A 30.1 (1.4)	^B 9.3 (0.7)
Snag density (stems/ha)	^A 17.3 (11.3)	^A 21.6 (3.1)	^A 39.4 (7.9)
Snag diameter (cm)	^A 26.7 (6.2)	^A 18.9 (1.3)	^A 21.4 (2.0)
Snag basal area (m ² /ha)	^A 0.8 (0.4)	^A 0.6 (0.1)	^A 1.3 (0.2)
Canopy cover (%)	^A 91.0 (1.3)	^A 89.1 (1.9)	^B 73.5 (2.9)
Shrub cover (%)	^A 50.3 (14.9)	^A 50.6 (5.6)	^A 71.2 (4.4)
CWD (natural log [m ³ /ha])	^A 1.15 (0.03)	^A 1.11 (0.04)	^B 0.84 (0.04)
Litter depth (cm)	^A 6.1 (1.6)	^A 6.0 (0.3)	^B 2.7 (0.2)
Woodrat houses (no./ha)	^A 22.5 (8.7)	^A 18.8 (4.2)	^A 45.7 (8.5)

* n = 9 for tree density, tree diameter, and tree basal area.

^{A, B} Sites sharing a common letter are not significantly different for a given attribute (Ryan's Q test, $\alpha = 0.05$).

Birds

At site LR, the most abundant bird species were the oak titmouse (*Baeolophus inornatus*), bushtit (*Psaltriparus minimus*), house finch (*Carpodacus mexicanus*), lesser goldfinch (*Carduelis psaltria*), western scrub-jay (*Aphelocoma californica*), and dark-eyed junco (*Junco hyemalis*) (table 3). At site HR2, the most abundant species were the chestnut-backed chickadee (*Parus rufescens*), Steller's jay (*Cyanocitta stelleri*), dark-eyed junco, and orange-crowned warbler (*Vermivora celata*) (table 3). Total abundance of all species, species richness, and Shannon-Wiener diversity index were all significantly higher at site LR (table 3, $P < 0.05$). Of the eight focal conservation species identified in the Oak Woodland Bird Conservation Plan (CalPIF 2002), seven were significantly more abundant at site LR (table 3, $P < 0.05$).

Table 3—Mean values (and standard errors) of bird species abundance and species diversity on 50-m-radius plots in oak woodlands at high risk (HR1, HR2) and low risk (LR) of SOD infection, San Luis Obispo County, California. Five annual visits were made to each plot during March-June, 2002 and 2003. The following species are listed below: a) the 10 most abundant species at each site, and b) focal conservation species identified in CalPIF (2002).

	HR2 (n = 42)	LR (n = 98)
Species abundance (maximum no. individuals/single visit)		
All species	24.1 (0.8)	34.6 (0.8) **
# Acorn woodpecker (<i>Melanerpes formicivorus</i>)	0.1 (0.1)	0.8 (0.1) **
Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)	0.0 (0.0)	1.4 (0.1) **
# Blue-gray gnatcatcher (<i>Polioptila caerulea</i>)	0.0 (0.0)	0.7 (0.1) **
Brown creeper (<i>Certhia americana</i>)	1.1 (0.1) **	0.0 (0.0)
Bushtit (<i>Psaltriparus minimus</i>)	0.8 (0.2)	2.5 (0.3) **
Chestnut-backed chickadee (<i>Poecile rufescens</i>)	2.8 (0.4) **	0.3 (0.1)
Dark-eyed junco (<i>Junco hyemalis</i>)	2.2 (0.2)	2.3 (0.2)
House finch (<i>Carpodacus mexicanus</i>)	0.1 (0.0)	2.5 (0.2) **
Hutton's vireo (<i>Vireo huttoni</i>)	1.3 (0.1)	1.3 (0.1)
# Lark sparrow (<i>Chondestes grammacus</i>)	0.1 (0.0)	0.5 (0.1) **
Lesser goldfinch (<i>Carduelis psaltria</i>)	0.3 (0.1)	3.3 (0.2) **
# Nuttall's woodpecker (<i>Picoides nuttallii</i>)	0.4 (0.1)	0.8 (0.1) **
# Oak titmouse (<i>Baeolophus inornatus</i>)	0.9 (0.1)	3.6 (0.1) **
Orange-crowned warbler (<i>Vermivora celata</i>)	2.1 (0.2) **	0.1 (0.0)
Pacific-slope flycatcher (<i>Empidonax difficilis</i>)	1.3 (0.1) **	0.1 (0.0)
Spotted towhee (<i>Pipilo maculatus</i>)	1.6 (0.2) *	1.2 (0.1)
Steller's jay (<i>Cyanocitta stelleri</i>)	2.6 (0.2) **	0.0 (0.0)
Violet-green swallow (<i>Tachycineta thalassina</i>)	0.2 (0.1)	1.8 (0.1) **
Warbling vireo (<i>Vireo gilvis</i>)	1.3 (0.2) **	0.0 (0.0)
# Western bluebird (<i>Sialia mexicana</i>)	0.0 (0.0)	1.1 (0.1) **
# Western scrub-jay (<i>Aphelocoma californica</i>)	0.3 (0.1)	2.5 (0.1) **
# Yellow-billed magpie (<i>Pica nuttalli</i>)	0.0 (0.0)	0.1 (0.0)
Species richness (no. of species per point-count location)	14.3 (0.5)	17.2 (0.3) **
Shannon-Wiener diversity index	2.50 (0.04)	2.64 (0.02) **

Identified as focal species in Oak Woodland Bird Conservation Plan (CalPIF 2002).

* Difference between sites statistically significant at $P < 0.05$ (Mann-Whitney U test).

** Difference between sites statistically significant at $P < 0.01$ (Mann-Whitney U test).

Small Mammals

Total small mammal abundance was much greater on both HR sites than on site LR (*table 4*). Among the commonly captured species, the dusky-footed woodrat, brush mouse (*Peromyscus boylii*), and California mouse (*P. californicus*) were all more abundant at sites HR1 and HR2 than at site LR (*table 4*, $P < 0.05$). Brush mice were particularly abundant at site HR1, being three times more abundant than at site HR2 and 10 times more abundant than at site LR (*table 4*). Only the piñon mouse (*P. truei*) was more abundant at site LR than either HR site (*table 4*, $P < 0.05$). Species diversity was similar at all three sites, both in terms of species richness and the Shannon-Wiener diversity index (*table 4*).

Table 4—Mean values (and standard errors) of small mammal abundance (minimum number of animals) and species diversity on 1.1-ha trapping grids in oak woodlands at high risk (HR1, HR2) and low risk (LR) of SOD infection, San Luis Obispo County, California. Three trapping sessions were conducted on each grid (spring 2003, fall 2003, spring 2004). Each trapping session lasted for 3 consecutive nights.

	HR1 (n = 9)	HR2 (n = 17)	LR (n = 66)
Species abundance (minimum no. animals per grid)			
All species	^A 86.2 (6.0)	^B 47.6 (4.2)	^C 24.1 (1.4)
Brush mouse (<i>Peromyscus boylii</i>)	^A 46.0 (10.0)	^B 14.1 (1.9)	^C 4.3 (0.5)
California mouse (<i>P. californicus</i>)	^A 12.9 (1.3)	^A 15.3 (2.3)	^B 1.5 (0.3)
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	^A 20.8 (4.8)	^A 16.8 (1.4)	^B 9.0 (0.7)
Piñon mouse (<i>P. truei</i>)	^B 1.0 (0.7)	^B 0.0 (0.0)	^A 7.0 (0.6)
Species richness (no. of species per grid)	^A 4.22 (0.14)	^A 3.88 (0.21)	^A 3.79 (0.15)
Shannon-Wiener diversity index	^A 1.05 (0.10)	^A 1.12 (0.03)	^A 1.08 (0.03)

^{A, B, C} Sites sharing a common letter are not significantly different for a given attribute (Ryan's Q test, $\alpha = 0.05$).

Both male and female dusky-footed woodrats were significantly heavier on sites HR1 and HR2 than site LR (*table 5*, $P < 0.05$). Male and female California mice body masses were also higher at sites HR1 and HR2 than site LR, although the difference was significant only for site HR1 (*table 5*, $P < 0.05$). We detected no significant differences in body mass among study sites for male or female brush mice (*table 5*).

Table 5— Mean body masses (and standard errors) in grams of 3 small mammal species trapped on 1.1-ha trapping grids in oak woodlands at high risk (HR1, HR2) and low risk (LR) of SOD infection, San Luis Obispo County, California. Trapping was conducted during spring 2003, fall 2003, and spring 2004.

	Body mass (g)		
	HR1*	HR2*	LR*
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)			
Male (<i>n</i> = 419)	^A 243.5 (4.3)	^A 239.2 (3.8)	^B 218.7 (3.2)
Female (<i>n</i> = 521)	^A 214.0 (3.4)	^A 213.2 (3.6)	^B 196.7 (1.9)
California mouse (<i>Peromyscus californicus</i>)			
Male (<i>n</i> = 203)	^A 37.2 (0.5)	^{A B} 36.4 (0.4)	^B 35.1 (0.6)
Female (<i>n</i> = 197)	^A 40.5 (0.8)	^B 38.3 (0.5)	^B 36.7 (0.9)
Brush mouse (<i>P. boylii</i>)			
Male (<i>n</i> = 408)	^A 21.9 (0.2)	^A 22.2 (0.2)	^A 22.0 (0.2)
Female (<i>n</i> = 423)	^A 22.5 (0.3)	^A 22.1 (0.3)	^A 21.9 (0.3)

^{A, B} Sites sharing a common letter are not significantly different for a given attribute (Ryan's Q test, $\alpha = 0.05$).

Amphibians and Reptiles

During 2002, amphibian abundance was nearly eight times greater at site HR2 than site LR (table 6, $P < 0.05$), mainly due to the Monterey salamander (*Ensatina eschscholtzii eschscholtzii*). Monterey salamanders were abundant on site HR2, but absent from site LR. Slender salamanders (*Batrochoseps* spp.) were more abundant on site HR2 (table 6, $P < 0.10$), although the difference was not significant at our specified α level of 0.05. In addition, species richness and the Shannon-Wiener diversity index were significantly higher at site HR1 (table 6, $P < 0.05$). In contrast, reptiles were observed almost exclusively on the LR site (table 6). While we recorded 10 reptile species at site LR (three lizard, one skink, and six snake spp.), we observed only one reptile species at site HR1 (western fence lizard [*Sceloporus occidentalis*]).

Table 6—Mean values (and standard errors) of amphibian and reptile species abundance and diversity on study sites containing oak woodlands at high risk (HR2) and low risk (LR) of SOD infection, San Luis Obispo County, California. Sampling was conducted during January-May 2002. The maximum numbers of animals observed per grid on the LR site were divided by 4.25 to account for a larger grid size at site LR (136 coverboards per grid at site LR, 32 coverboards per grid at site HR2).

	HR2 (n = 5)	LR (n = 8)
Amphibians		
Species abundance (maximum no. individuals/single visit)		
All species	17.8 (4.7) **	2.3 (0.8)
Monterey salamander (<i>Ensatina e. eschscholtzii</i>)	12.6 (3.8) **	0.0 (0.0)
Slender salamander (<i>Batrochoseps</i> spp.)	4.6 (2.1)	2.2 (0.8)
Species richness (no. of species per grid)	2.4 (0.2) *	1.4 (0.2)
Shannon-Wiener diversity index	0.62 (0.12) *	0.13 (0.07)
Reptiles		
Species abundance (maximum no. individuals/single visit)		
All species	0.2 (0.2)	6.9 (1.0) **
California legless lizard (<i>Anniella pulchra</i>)	0.0 (0.0)	1.2 (0.6) *
Southern alligator lizard (<i>Gerrhonotus multicarinatus</i>)	0.0 (0.0)	0.4 (0.1) *
Western fence lizard (<i>Sceloporus occidentalis</i>)	0.2 (0.2)	1.7 (0.3) **
Western skink (<i>Eumeces skiltonianus</i>)	0.0 (0.0)	3.1 (0.5) **
Snakes (all snake species)	0.0 (0.0)	0.6 (0.1) *
Species richness (no. of species per grid)	0.2 (0.2)	5.8 (0.6) **
Shannon-Wiener diversity index	0.00 (0.00)	1.20 (0.09) **

* Difference between sites statistically significant at $P < 0.05$ (Mann-Whitney U test).

** Difference between sites statistically significant at $P < 0.01$ (Mann-Whitney U test).

During 2004, the amphibian and reptile communities were similar on sites HR1 and HR2. No comparison between sites HR1 and HR2 for any species or group of amphibians or reptiles was significant (table 7). Species richness and the Shannon-Wiener diversity index were also similar for both amphibians and reptiles at each site (table 7). As in 2002 at site HR1, amphibians were observed frequently, but few reptiles were found (tables 6 and 7).

Table 7— Mean values (and standard errors) of amphibian and reptile species abundance and diversity on study sites containing oak woodlands at high risk (HR1, HR2) of SOD infection, San Luis Obispo County, California. Sampling was conducted during January-May 2004. No attributes were significantly different between study sites ($P < 0.05$, Mann-Whitney U test).

	HR1 ($n = 5$)	HR2 ($n = 3$)
Amphibians		
Species abundance (maximum no. individuals/single visit)		
All species	26.4 (8.2)	20.7 (0.7)
Monterey salamander (<i>Ensatina eschscholtzii</i>)	17.4 (6.3)	18.3 (1.5)
Slender salamander (<i>Batrachoseps</i> spp.)	8.8 (3.1)	2.3 (0.9)
Species richness (no. of species per grid)	2.2 (0.2)	2.0 (0.0)
Shannon-Wiener diversity index	0.60 (0.05)	0.34 (0.09)
Reptiles		
Species abundance (maximum no. individuals/single visit)		
All species	0.6 (0.4)	0.3 (0.3)
California legless lizard (<i>Anniella pulchra</i>)	0.0 (0.0)	0.0 (0.0)
Southern alligator lizard (<i>Gerrhonotus multicarinatus</i>)	0.2 (0.2)	0.3 (0.3)
Western fence lizard (<i>Sceloporus occidentalis</i>)	0.4 (0.2)	0.0 (0.0)
Western skink (<i>Eumeces skiltonianus</i>)	0.0 (0.0)	0.0 (0.0)
Snakes (all snake species)	0.0 (0.0)	0.0 (0.0)
Species richness (no. of species per grid)	0.6 (0.4)	0.3 (0.3)
Shannon-Wiener diversity index	0.14 (0.14)	0.00 (0.00)

Discussion

Differences Between Low-Risk and High-Risk Sites

Compared to the low-risk site, more moderate annual temperatures and over 1.6 times the rainfall characterized our San Luis Obispo sites at high risk of SOD infection (table 1). Warm, wet winters typify coastal oak woodlands in California at high risk of SOD (Major 1988, Rizzo and Garbelotto 2003). These climatic conditions are largely responsible for the habitat differences that we observed between our low-risk and high-risk study sites. Our low-risk study site contained more open stands of smaller trees (predominately blue oak), somewhat more shrub cover, but much less downed wood and litter. Our high-risk study sites were

characterized by stands of larger trees (predominately coast live oak and California bay) with a dense canopy, somewhat more open understory, large amounts of downed wood, and a well-developed litter layer. We surmise that these structural differences in vegetation between the low-risk and high-risk study sites were primarily responsible for the observed differences in the small vertebrate communities.

Birds were more abundant and diverse in low-risk habitat than high-risk habitat. This result surprised us because more complex overstory at the surveyed high-risk site should have provided additional niches for bird species, as proposed by MacArthur and MacArthur (1961). Horizontal habitat patchiness, however, was greater on the low-risk site, which contained a more heterogeneous mosaic of woodland, grassland, and chaparral (personal observation). In addition, the understory was more developed at the low-risk site, as indicated by greater shrub cover. Both of these factors may have contributed to a more diverse avian community at the low-risk site (Roth 1976). Each habitat type had distinct avian communities with some species being much more abundant in one habitat type than the other. The surveyed high-risk site had low numbers of the eight focal conservation species identified by CalPIF (2002), relative to the low-risk site. The chestnut-backed chickadee, Steller's jay, orange-crowned warbler, Pacific-slope flycatcher (*Empidonax difficilis*), warbling vireo (*Vireo gilvis*), Wilson's warbler (*Wilsonia pusilla*), and Cassin's vireo (*Vireo cassinii*), however, were found only or predominantly at the high-risk site.

Small mammals were much more abundant in the high-risk habitat, and some species (particularly the dusky-footed woodrat) were in better physical condition, as measured by body mass. High-risk habitat characteristics that likely contributed to these differences include greater amounts of water, food (larger and more numerous oak trees), vertical habitat structure, and downed wood. For example, in a prior study on our low-risk study site (Tietje and others 1997), the abundance of woodrats, piñon mice, brush mice, and California mice all were positively and strongly correlated with tree canopy, and cover of shrubs and downed wood. Because some small mammal populations are characterized by cycles lasting 3-4 years (Boonstra and others 1998), we investigated the possibility that population cycles at the low-risk and high-risk sites were asynchronous during our study (in effect, low-risk site at low point in cycle, high-risk sites at peak in cycle) by examining our unpublished data from Camp Roberts. We found that total small mammal population densities were never as great at Camp Roberts during 1993-2002 as they were at the high-risk sites during this study.

The greater abundance of amphibians (primarily salamanders) in high-risk habitat and of reptiles (primarily lizards) in low-risk habitat can be attributed to a combination of climatic and habitat conditions. In terms of climate, the wetter winters and cooler summers of the high-risk sites are more favorable for amphibians than reptiles. Block and Morrison (1998) also found that mesic sites supported more amphibians and fewer reptiles than xeric, blue-oak-dominated sites in the Sierra Nevada and Tehachapi Mountains. In terms of habitat, Monterey salamander and slender salamander abundances in the Pacific Northwest were positively correlated with litter depth and downed wood volume (Corn and Bury 1991, Aubry and Hall 1991). These two habitat elements protect salamanders from desiccation and predators and provide them with foraging habitat (California Department of Fish and Game 2002, Wisely and Golightly 2003). Although litter depth and downed wood are also important for reptile species such as the western fence lizard and western skink (*Eumeces skiltonianus*), they prefer more open areas and generally avoid densely forested areas (California Department of Fish and Game 2002).

Potential bias in our results may have been introduced by differences in species detectability between the low-risk and high-risk sites. Detectability may have been particularly important with respect to birds where between-site differences in the bird community and habitat structure may have influenced detectability (Boulinier and others 1998). As a result, our observations of avian abundance and species richness may have been biased if detection probabilities were higher at the low-risk site. With respect to small mammals, we believe that by marking individuals we controlled potential bias to a large degree. We generally observed that most captures on the final night of a trapping session were recaptures, and thus, the minimum number of animals captured was a robust index for the true population density. With respect to amphibians and reptiles, the observed differences in abundance were so large between the high-risk and low-risk sites that we believe the differences to be genuine.

Although low-risk habitat is widespread in San Luis Obispo County (Meentemeyer and others 2004), we sampled only one location. Camp Roberts, our low-risk site, contains well-structured, relatively undisturbed blue oak-coast live oak woodlands (Tietje and others 1997). Combined with our casual observations of low-risk habitat throughout the county, we believe that Camp Roberts contains above-average wildlife habitat for low-risk portions of the county. Thus, we believe that small mammals and amphibians are more abundant in high-risk habitat than low-risk habitat throughout the county. On the other hand, birds and reptiles may not be as abundant at other low-risk habitat sites as they were at Camp Roberts.

Implications of SOD for San Luis Obispo County Wildlife

If SOD infects coastal oak woodlands within the county, impacts to the structure and composition of these woodlands will vary according to the time scale under consideration. In the short term (perhaps 5-30 years after infection), we would expect the generation of large amounts of CWD from stem failure of dying coast live oak trees (Swiecki and Bernhardt this volume), a reduction in the density of tree-sized stems, and the creation of canopy gaps leading to patches of increased shrub growth. The impacts of such major habitat changes on wildlife will be species-specific and are difficult to predict. Some small mammal species might benefit from an increase in downed wood and shrub growth, but the loss of vertical habitat structure could outweigh any benefits. Similarly, salamanders might be adversely affected by canopy gaps that result in warmer, drier microclimates and reduced amounts of leaf litter (deMaynadier and Hunter 1995), but the increase in downed wood might mitigate these impacts.

In the long term, we would expect California bay trees to replace many of the dead coast live oak trees in the forest canopy (Brown and Allen-Diaz this volume). We found few reports on wildlife use of California bay trees in the ecological literature. Dusky-footed woodrats, California mice, and western gray squirrels (*Sciurus griseus*) consume the fruit of California bay trees (Linsdale and Tevis 1951, Stienecker and Browning 1970, Merritt 1974), and woodrats use California bay cuttings and leaves for house construction and nest lining (Linsdale and Tevis 1951, Hemmes and others 2002). On the other hand, California bay trees have fewer cavities for nesting birds compared to coast live oaks (Winslow and Tietje this volume), are used less frequently than coast live oaks by foraging birds (Apigian and Allen-Diaz this volume), and contain monoterpenoid compounds that may deter the consumption of bay leaves by deer and other herbivores (Goralka and others 1996). Given the well-documented use of oak trees by many wildlife species for food, cover, and reproduction (Barrett 1980, Block and Morrison 1987, Pavlik and others 1991, CalPIF 2002), we would expect long-term negative impacts on most wildlife species if California bay largely replaced coast live oak in the forest canopy.

High-risk habitat in San Luis Obispo County is relatively scarce and fragmented in distribution. A reduction in habitat quality, therefore, could threaten populations of species that are particularly abundant in or restricted to high-risk woodlands. The dusky-footed woodrat is perhaps the most ecologically important species in high-risk woodlands, and a decline in its population could impact a wide range of species that prey upon woodrats or utilize woodrat houses for shelter and foraging (Linsdale and Tevis 1951). In addition, dusky-footed woodrats are the major food item for the California spotted owl (*Strix occidentalis occidentalis*) in coastal oak woodlands

(Verner and others 1992), which provide the preponderance of suitable owl habitat west of the Sierra Nevada. Several other bird species may be largely restricted to high-risk habitat within the county (see above), and we would expect at least one of these species (the chestnut-backed chickadee) to be adversely affected by the loss of coast live oaks (Apigian and Allen-Diaz this volume). Finally, Monterey and slender salamanders may be particularly susceptible to SOD impacts because they would be less capable of dispersal to nearby uninfected stands. The Monterey salamander was abundant on our high-risk study sites and coastal oak woodlands likely constitute its primary habitat within the county. Several slender salamander species (*Batrachoseps* spp.) occur within the county, at times within a few km of each other (Jockusch and Wake 2002). Even localized occurrences of SOD may lead to the isolation and loss of *Batrachoseps* species populations with highly localized distributions (see for example, Bradford and others 1993).

Should SOD become established in San Luis Obispo County, natural resource managers and land-use planners will be challenged to protect the county's coastal oak woodlands. This study provides a better understanding of the distinctive habitat and wildlife communities found in these woodlands. Our results could potentially serve as baseline data should SOD spread to the coastal oak woodlands of San Luis Obispo County.

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