

# Predictive Occurrence Models for Bat Species in California

ANDREW A. DUFF,<sup>1,2</sup> *Department of Biology, Ball State University, Muncie, IN 47306, USA*

THOMAS E. MORRELL,<sup>3</sup> *Department of Biology, Ball State University, Muncie, IN 47306, USA*

**ABSTRACT** The ability to accurately predict the potential occurrence of species of management concern is useful for wildlife managers, particularly for those whose management activities involve large areas where sampling is difficult due to logistical or financial constraints. During the summers of 2002 and 2003, we used mist nets to capture bats (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) in Whiskeytown National Recreation Area in north-central California, USA. We used landscape-scale variables, logistic regression, and Akaike's Information Criterion (AIC) to model species distributions and produce spatially discerning predictive occurrence maps. We developed a priori models that we used to determine which landscape-scale variables best discriminated between capture sites and non-capture sites. The odds of capturing a bat were 3.3 greater when total edge increased by 10,000 m, whereas for Yuma myotis (*Myotis yumanensis*), the odds of predicting presence were 0.2 greater when distance to lakes and ponds decreased by 2,000 m. Elevation was important in predicting the distribution of silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*). Increasing elevation by 400 m decreased the odds of capturing a silver-haired bat by 0.1 and a big brown bat by 0.4. Classification accuracy for our models ranged from 80.9% for all bat species combined to 72.3% for Yuma myotis and silver-haired bats. Predictive occurrence models can be valuable to bat conservation efforts because they provide spatial data important for evaluating the effects of management activities on species distributions. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):693–700; 2007)

DOI: 10.2193/2005-692

**KEY WORDS** bats, big brown bat, California, *Eptesicus fuscus*, *Lasionycteris noctivagans*, logistic regression, *Myotis yumanensis*, predicting species occurrence, silver-haired bat, Yuma myotis.

Bats can present a number of difficulties in assessing and monitoring trends in their populations (O'Shea and Bogan 2003). Information regarding basic natural history, distribution, roosting preferences, and colony locations are poorly known for many bat species. Due to vagility and nocturnal activity patterns, inventory and monitoring of bat species distributions can be problematic. Nevertheless, many managers would be interested in an effective landscape-scale approach for detecting species occurrence. Furthermore, data on the distribution of bats enables resource managers to make informed decisions regarding forest use and land management (Morrell et al. 1999, Morrell and Duff 2005). Baseline inventories are essential for biologists to monitor population trends and evaluate population responses to management activities. However, because of lack of information, resource managers are often unable to predict if proposed land uses will affect bat populations.

Researchers have developed spatially explicit predictive distribution models for a variety of animals (e.g., Augustin et al. 1996 [deer], Manel et al. 1999 [Himalayan river birds], Gabler et al. 2000 [pigmy rabbits], Fleishman et al. 2001 [butterflies], Nicolas et al. 2002 [amphibians]). Predictive models are relevant even for highly mobile organisms; however, model stability and agreement tend to decrease for more widespread species (Jaberg and Guisan 2001). Although quantification of species–environment relationships represents the core of predictive geographical model-

ing in ecology (Guisan and Zimmermann 2000), such work with bats has been limited (Jaberg and Guisan 2001; D. A. Keinath, Bighorn Canyon National Recreation Area, unpublished data). Elevation and vegetation structure were landscape-scale variables used for predicting bat distribution in the Jura Mountains, Switzerland; however, predictive efficacy varied among species (Jaberg and Guisan 2001). Modeling relationships between the distribution of bats and landscape-scale parameters presents a considerable challenge, but landscape structures are valuable to predict bat distribution or to identify areas of important biological significance (Jaberg and Guisan 2001).

The objectives of our study were to 1) evaluate species distributions with respect to biotic and abiotic landscape-scale patterns and 2) develop predictive models of species occurrence based on landscape-scale parameters.

## STUDY AREA

Whiskeytown National Recreation Area (WHIS) is a 17,000-ha park located 13 km west of Redding, Shasta County, California, USA. Elevations ranged from 256 m to 1,889 m. Predominant trees species found at WHIS included black oak (*Quercus kelloggii*), canyon live oak (*Q. chrysolepis*), knobcone pine (*Pinus attenuata*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Chaparral areas consisted mainly of manzanita (*Arctostaphylos* spp.) and ceanothus (*Ceanothus* spp.). Montane chaparral species included the shrub form of tanoak (*Lithocarpus densiflorus* var. *echinoides*) and bush chinquapin (*Chrysolepis sempervirens*). Whiskeytown Lake, a man-made reservoir 1,303 ha in area with 57.9 km of shoreline, constituted 7.7% of the park area. Mean annual maximum

<sup>1</sup> E-mail: [duffaad@dfw.wa.gov](mailto:duffaad@dfw.wa.gov)

<sup>2</sup> Present address: Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012-1541, USA

<sup>3</sup> Present address: Science, Math, and Engineering Division, Imperial Valley College, 380 East Aten Road, Imperial, CA 92251, USA

**Table 1.** Landscape-scale variables used in logistic regression modeling to predict bat species (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) occurrence at Whiskeytown National Recreation Area, California, USA, 2002 and 2003.

Variable	Definition
Total edge <sup>a,b</sup>	Total linear edge (m) within a 1,500-m-radius plot
Patch richness	Patch richness (no. of different cover types) within a 1,500-m radius
$\bar{x}$ summer temp	Mean summer (May, Jun, Jul, Aug 1980–1997) temp (°C)
Total summer precipitation	Total summer (May, Jun, Jul, Aug 1980–1997) precipitation (cm)
Riparian flyways <sup>a,c</sup>	Riparian flyways (m) within a 1,500-m-radius plot
Terrestrial flyways	Terrestrial flyways (m) within a 1,500-m-radius plot
Distance to nearest stream	Distance to nearest stream (m)
Distance to nearest lake or pond <sup>d</sup>	Distance to nearest lake or pond (m)
Canopy closure	% patch crown closure derived from aerial photography
Tree size <sup>b,c,d</sup>	Patch overstory tree size derived from aerial photography (cm dbh)
Elevation <sup>a,b,c,d</sup>	Elevation (m)

<sup>a</sup> Used in all-species model set.

<sup>b</sup> Used in big brown bat model set.

<sup>c</sup> Used in silver-haired bat model set.

<sup>d</sup> Used in Yuma myotis model set.

and minimum temperatures were 23.4° C, 9.2° C, respectively, and total precipitation was 148.0 cm at WHIS during 2002 and 2003 (Western Regional Climate Center 1999).

## METHODS

We conducted bat surveys using mist nets between June and August 2002–2003. We captured bats at 47 sites, including ponds, streams, and Whiskeytown Lake, as well as narrow canyons, along secondary roads, and hiking trails below the forest canopy. We partitioned sampling efforts spatially in all representative habitats and across elevational gradients while maximizing capture probabilities (netting over smooth water in aquatic sites or in locations with multiple corridors for commuting and foraging bats in terrestrial sites). We set 1–6 mist nets at each sampling site before sunset, and they remained in place until at least midnight. When we sampled a site more than once, we allowed  $\geq 10$  days to pass before we netted again. We visited netting sites 1–3 times during the study. We identified, sexed, weighed, and released all captured bats.

We created a Geographic Information System (GIS) database (resolution = 30 m) in ArcGIS Desktop Version 8.3, 2003, which included 11 landscape-scale variables for the study area (Table 1). We collected geographic coordinates for all netting sites using a Garmin 12XL Global Positioning System (GPS;  $\pm 15$ -m accuracy). We derived the GIS layers that constituted our landscape-scale variables from existing state and federal GIS databases.

We measured 4 variables within a 1,500-m-radius circular plot centered on the netting site. We selected a 1,500-m radius because this area falls approximately in the middle of reported home range sizes of bat species known to occur in the study areas (Zeiner 1990, Verts and Carraway 1998). Total edge and patch richness were moving window landscape metrics calculated with FRAGSTATS Version 3.3, 2003. We used FRAGSTATS to obtain a value for each metric at the landscape level. We based landscape metrics, total edge and patch richness, upon the number and

type of cover categories occurring within a plot. Total edge represented linear edge (m) occurring in a plot. Patch richness was the number of cover types occurring within a plot (agriculture, barren or rock or snow, conifer forest and woodland, hardwood forest and woodland, herbaceous vegetation, mixed conifer or hardwood forest and woodland, shrubland vegetation, urban or residential areas; California Vegetation [CALVEG] 2002). We created terrestrial flyway and riparian flyway indices with line statistic moving window analyses in ArcGIS Spatial Analyst using data from Klamath Network Inventory and Monitoring Program GIS database (KLMNGIS 2002). Terrestrial flyways represented bat corridors as linear length (m) of all dirt and gravel roads and trails in a plot, whereas riparian flyways represented linear length (m) of all natural and man-made rivers and streams within a plot.

Seven remaining spatial variables we measured at each sampling site included total summer precipitation, mean summer temperature, distance to nearest stream, distance to nearest lake or pond, percent crown closure, overstory tree size, and elevation. We obtained total summer precipitation and mean summer temperature from the DAYMET 1980–1997 climatological summaries (Thornton et al. 1997, DAYMET 2003). The DAYMET data set was one of the few climatic data sets available at the landscape scale. Data covering the entire study area were necessary for all of the model variables to allow the application of our results to the landscape to produce maps. We combined long-term (18-yr  $\bar{x}$ ) climatological data sets for months in which we trapped bats (May, Jun, Jul, and Aug) to produce the surfaces used in our analysis. We created total summer precipitation by summing 4 monthly data layers, and we created mean summer temperature by summing 4 monthly data layers and dividing by 4. We determined distance to nearest stream and distance to nearest lake or pond using ArcGIS Spatial Analyst Euclidian distance function. Lakes and ponds consisted of all water bodies  $\geq 0.15$  ha. We derived canopy closure from a geometric optical canopy model that estimated canopy closure within each tree stand as a percent

cover value (CALVEG 2002). We evaluated the resulting estimates of canopy closure using aerial photography, and we subsequently corrected any errors in a GIS environment. We generated overstory tree size estimates from Landsat TM imagery using a combination of supervised and unsupervised image classification techniques in conjunction with aerial photography. We expressed canopy closure (%) as 1 of 11 classes: 0, 0–9, 10–19, 20–29, 30–39, 40–49, 50–59, 60–69, 70–79, 80–89, 90–100; and we expressed tree size (cm dbh) as 1 of 6 classes (no trees present, <2.5, 2.5–27.9, 28.0–40.6, 40.7–70, >70; CALVEG 2002). We used arcsine transformations to approximate a normal distribution for canopy closure percentages before analysis. We obtained elevation from United States Geological Survey digital elevation models (MapMart Interactive Data Warehouse 2002).

We used logistic regression to determine which variables best discriminated between sites where we captured bats (species or species group) and sites where we did not capture them. The binary outcome of our logistic regression analysis was bat presence at a site ( $n = 47$ ) during the summer 2002–2003. We did not differentiate between genders or ages of bats in our analysis. We developed, a priori, a global model for each species modeled that included variables we believed influenced bat distribution at the landscape level. We constructed our global models as follows: 1) all species combined (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasiurus noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) included elevation, total edge, and riparian flyways; 2) Yuma myotis contained distance to nearest lake or pond, elevation, and tree size; 3) silver-haired bats included elevation, riparian flyways, and tree size; and 4) big brown bats contained elevation, total edge, and tree size (Table 1). Using all-subsets selection and each global model, we generated 7 competing models for each species or species group (i.e., model set).

Once we developed the model sets, we performed binary logistic regressions in SPSS for Windows Version 11.5, 1999. We used Hosmer–Lemeshow goodness-of-fit (GOF) tests to evaluate the fit of the global model ( $P > 0.05$ ; Allison 1999). We used second-order Akaike's Information Criterion ( $AIC_c$ ) to select the most parsimonious regression model (as determined by  $AIC_c$  differences [ $\Delta_i$ ]; Burnham and Anderson 2002). We used model probabilities (Akaike wt [ $w_i$ ]) to determine which model best fit our capture data, assuming that one of the models in the model set must have been the best model (Burnham and Anderson 2002).

We based models selected to create predictive probability maps on model parsimony ( $AIC_c$ ),  $w_i$ , variable relative importance, and ecological relevance. However, we did not always use models with the lowest  $AIC_c$  for mapping if other competing models had low (<0.3)  $AIC_c$  differences. We used model-averaged estimates of variable coefficients (based on multi-model inference) to develop predictive probability occurrence maps. Model-averaged estimates of variable coefficients provide a more stabilized inference and

we calculated them by multiplying the variable coefficient by  $w_i$  and then summing this value across all models in the model set containing the variable (Burnham and Anderson 2002). We calculated unconditional sampling variances for the model coefficients in the most parsimonious model (unconditional sampling variance is an estimate of coeff. variance across the entire model set that is not conditional upon a particular model). We accomplished this using standard errors and  $w_i$  from models in the model set containing the coefficient variable. Additionally, we calculated unconditional confidence intervals using the model-averaged variable coefficients and standard errors. We rounded our results to account for biological and sampling reality.

We created predictive probability maps in ArcGIS 8 using map algebra in the Spatial Analyst raster calculator. We applied each model to every point (30-m raster cell) across the study area using the selected model with model-averaged coefficient estimates and logit equation (Allison 1999). We used nonparametric Mann–Whitney  $U$  tests a posteriori to determine significant differences ( $P < 0.05$ ) between capture versus non-capture sites for the 11 landscape-scale variables. We acknowledge a posteriori exploratory analyses cannot be taken with the same degree of confidence as those from confirmatory analyses using the information-theoretic approach, and to include  $P$ -values inappropriately mixes differing analysis paradigms (Burnham and Anderson 2002). We provide this information solely for researchers' consideration when addressing similar hypotheses in the future with a new and independent set of data.

## RESULTS

During the summers of 2002 and 2003, we captured 403 bats representing 10 species in mist nets during 77 nights. Five species accounted for 89.0% of the captures: Yuma myotis (27.8%), big brown bats (26.8%), silver-haired bats, (12.9%), California myotis (*Myotis californicus*; 11.2%), and Brazilian free-tailed bats (*Tadarida brasiliensis*; 10.2%). The remaining 11.0% of the captures included pallid bats (*Antrozous pallidus*; 4.7%), long-eared myotis (*M. evotis*; 3.2%), western red bats (*Lasiurus borealis*; 2.0%), hoary bats (*Lasiurus cinereus*; 1.2%), and fringed myotis (*M. thysanodes*; 0.7%). Approximately two-thirds of bats (67.5%) captured in WHIS were females. Because of this study, 7 new species were documented for park records: Yuma myotis, silver-haired bats, California myotis, long-eared myotis, red bats, hoary bats, and fringed myotis.

For all species combined, the model containing only total edge was most parsimonious ( $\Delta_i = 0$ ) and had a classification accuracy of 80.9% (Table 2). Unconditional sampling variance for the total edge coefficient was 0.1 (Table 3), and total edge provided the greatest relative importance in the model set (Table 4). The odds of capturing a bat were 3.3 greater when total edge increased by 10,000 m (Table 3). For all species combined, highest predicted probabilities (70–100%) of bat occurrence were areas with total edge

**Table 2.** Logistic regression model, percent correctly classified,  $-2 \log$  likelihood, number of estimable parameters ( $K$ ), and Akaike's Information Criterion (AIC<sub>c</sub>) differences ( $\Delta_i$ ), for modeling of bat species (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) occurrence from mist net captures at Whiskeytown National Recreation Area, California, USA, 2002 and 2003.

Species	Model	% correctly classified	$-2 \log$ likelihood	$K$	AIC <sub>c</sub> differences ( $\Delta_i$ )	Model probability ( $\omega_i$ )
All bat species	$1.3 + 1.2 \times \text{TE}^a$	80.9	42.9	3	0.000	0.43
	$1.4 + 1.0 \times \text{TE} + 0.5 \times \text{RF}$	80.9	41.7	4	1.242	0.23
	$1.3 - 0.2 \times \text{EL} + 1.3 \times \text{TE}$	80.9	42.6	4	2.141	0.15
	$1.2 - 0.8 \times \text{EL}$	78.7	46.6	3	3.707	0.07
	$1.4 - 0.1 \times \text{EL} + 1.0 \times \text{TE} + 0.5 \times \text{RF}$	80.9	41.7	5	3.721	0.07
	$1.3 - 0.6 \times \text{EL} + 0.5 \times \text{RF}$	78.7	45.4	4	4.872	0.04
Yuma myotis	$1.2 + 0.8 \times \text{RF}$	74.5	48.9	3	6.030	0.02
	$-1.2 - 1.6 \times \text{EL}$	68.1	51.3	3	0.000	0.30
	$-0.9 - 1.7 \times \text{DL}$	72.3	51.5	3	0.212	0.27
	$-1.2 - 1.6 \times \text{EL} - 1.0 \times \text{DL}$	66.0	49.9	4	0.922	0.19
	$-1.2 - 2.4 \times \text{EL} + 0.1 \times \text{TS}$	72.4	51.3	4	2.367	0.09
	$-0.9 - 1.7 \times \text{DL} + 0.003 \times \text{TS}$	72.3	51.5	4	2.606	0.08
Silver-haired bats	$-1.2 - 1.6 \times \text{EL} - 1.0 \times \text{DL} + 0.05 \times \text{TS}$	66.0	49.8	5	3.408	0.06
	$-0.5 - 0.1 \times \text{TS}$	61.7	62.5	3	11.150	0.001
	$-1.1 - 2.1 \times \text{EL}$	72.3	51.6	3	0.000	0.31
	$-1.0 + 0.6 \times \text{RF} - 1.7 \times \text{EL}$	68.1	49.3	4	0.106	0.29
	$-1.0 + 0.6 \times \text{RF} - 1.8 \times \text{EL} + 0.4 \times \text{TS}$	72.3	48.2	5	1.540	0.14
	$-1.2 + 0.3 \times \text{TS} - 2.5 \times \text{EL}$	72.3	50.8	4	1.668	0.13
Big brown bats	$-0.5 + 0.9 \times \text{RF}$	68.1	54.0	3	2.488	0.09
	$-0.6 + 1.0 \times \text{RF} + 0.3 \times \text{TS}$	66.0	53.2	4	4.066	0.04
	$-0.5 + 0.1 \times \text{TS}$	61.7	62.4	3	10.868	0.001
	$-1.2 - 0.9 \times \text{EL}$	74.5	50.3	3	0.000	0.41
	$-1.1 + 0.4 \times \text{TE}$	74.5	52.3	3	1.988	0.15
	$-1.3 + 0.2 \times \text{TS} - 0.9 \times \text{EL}$	74.5	50.1	4	2.184	0.14
Big brown bats	$-1.2 - 0.9 \times \text{EL} + 0.1 \times \text{TE}$	74.5	50.3	4	2.399	0.12
	$-1.1 + 0.2 \times \text{TS}$	74.5	53.3	3	2.993	0.09
	$-1.1 + 0.2 \times \text{TS} + 0.4 \times \text{TE}$	74.5	51.9	4	4.004	0.05
	$-1.3 + 0.2 \times \text{TS} - 0.9 \times \text{EL} + 0.1 \times \text{TE}$	74.5	50.0	5	4.608	0.04

<sup>a</sup> TE = total linear edge (m), RF = riparian flyways (m), EL = elevation (m), DL = distance to nearest lake or pond (m), TS = patch overstory tree size from aerial photography (cm).

>39,000 m (Fig. 1). A posteriori analyses showed mean differences at capture and non-capture sites for 5 variables were significant: total edge ( $P = 0.004$ ), elevation ( $P = 0.016$ ), terrestrial flyways ( $P = 0.017$ ), total summer precipitation ( $P = 0.030$ ), and distance to lakes and ponds ( $P = 0.036$ ; Table 5).

The model that contained only elevation was best fitting

for Yuma myotis, but failed the GOF test ( $P = 0.028$ ). The second best model ( $\Delta_i = 0.212$ ) included only distance to lakes and ponds, which increased classification accuracy by 4.3% (Table 2). Variance associated with the distance to lakes and ponds coefficient was 0.2 (Table 3). The odds of predicting Yuma myotis presence were 0.2 greater when distance to lakes and ponds decreased by 2,000 m (Table 3).

**Table 3.** Model variable, coefficient, unconditional sampling variance, lower and upper unconditional confidence interval for coefficient, Wald statistic, odds ratio, and lower and upper confidence interval on odds ratio for bat species (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) logistic regression modeling at Whiskeytown National Recreation Area, California, USA, 2002 and 2003.

Model	$B$	Unconditional sampling variance	Lower unconditional coeff. CI	Upper unconditional coeff. CI	Wald statistic	Odds ratio	Lower odds CI	Upper odds CI
All bat species								
Total edge	1.16	0.11	1.80	0.52	7.86	3.31	1.43	7.66
Yuma myotis								
Distance to nearest lake or pond	-1.73	0.20	-0.74	-2.37	5.98	0.18	0.05	0.71
Silver-haired bats								
Elevation	-2.10	0.12	-1.01	-3.10	4.17	0.10	0.01	0.91
Big brown bats								
Elevation	-0.89	0.22	-0.09	-1.68	1.75	0.41	0.11	1.53

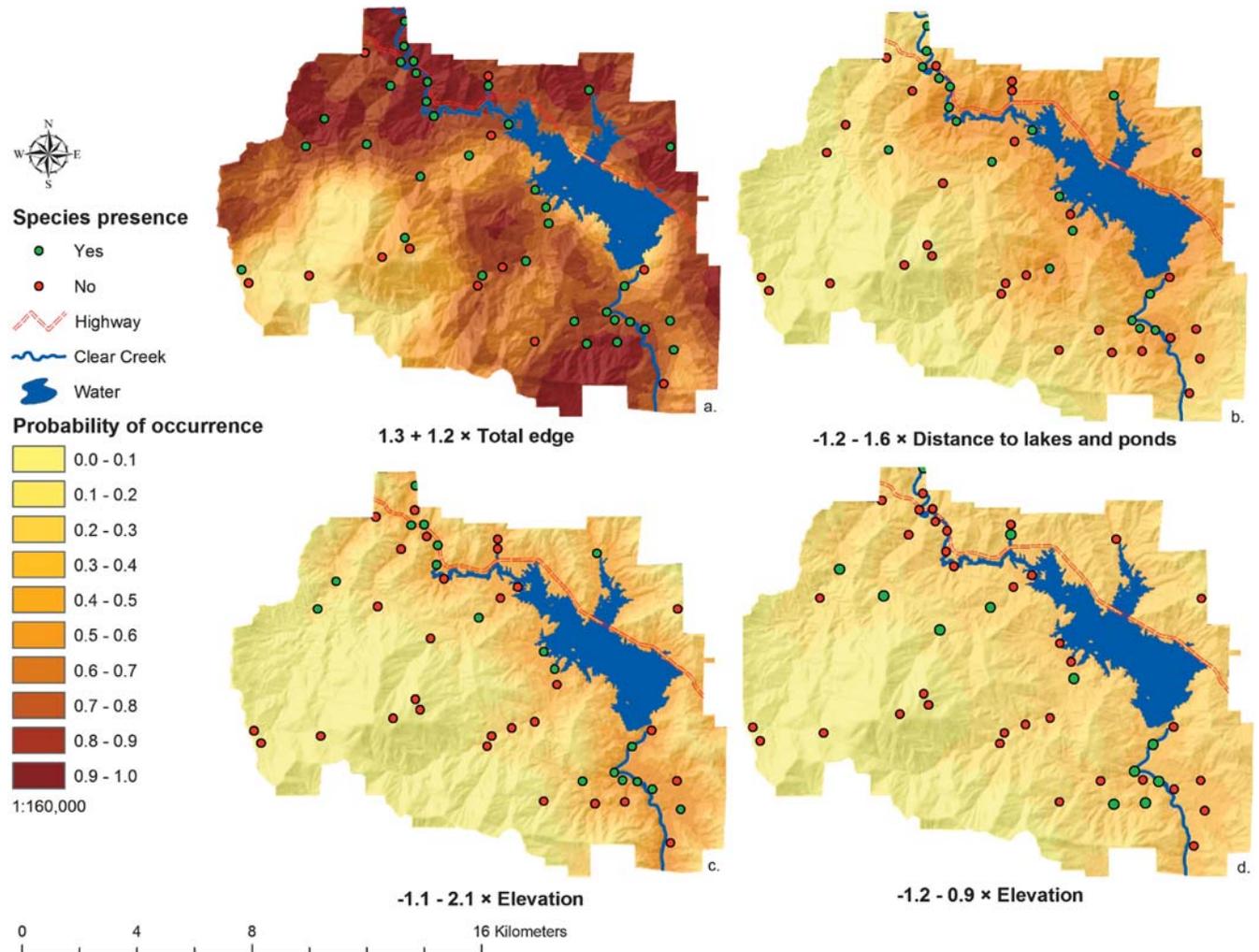
**Table 4.** Species and relative variable importance values (variable importance in the context of the model set, calculated by summing the Akaike weights over all models including the given variable) for each variable used in bat species (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) logistic regression modeling in Whiskeytown National Recreation Area, California, 2002 and 2003.

Species	Total edge	Tree size	Distance to nearest lake or pond	Elevation	Riparian flyways
All bat species	0.87	0.00	0.00	0.32	0.36
Yuma myotis	0.00	0.23	0.60	0.64	0.00
Silver-haired bats	0.00	0.32	0.00	0.87	0.55
Big brown bats	0.35	0.34	0.00	0.72	0.00

Highest predicted probabilities of occurrence (50–70%) for Yuma myotis were in areas where distance to lakes and ponds were <800 m (Fig. 1). A posteriori analyses showed mean differences at capture and non-capture sites for 4 variables were significant: distance to lakes and ponds ( $P = 0.003$ ), elevation ( $P = 0.006$ ), patch richness ( $P = 0.014$ ), and canopy closure ( $P = 0.049$ ; Table 5).

The model that contained elevation was most parsimo-

nious for silver-haired bats (Table 2), although the model that included elevation and riparian flyways had low AIC<sub>c</sub> differences. The elevation model provided the highest classification accuracy (Table 2). Variance for the elevation coefficient was 0.1 (Table 3). The odds of capturing a silver-haired bat decreased 0.1 when elevation increased by 400 m (Table 3). The highest predicted probabilities (40–70%) of occurrence of silver-haired bats were areas with elevation



**Figure 1.** Distribution maps produced from landscape-scale modeling using logistic regression with Akaike's Information Criterion (AIC<sub>c</sub>) selection for bat species at Whiskeytown National Recreation Area, California, USA, 2002 and 2003. (a) All species combined (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*), (b) Yuma myotis, (c) silver-haired bats, and (d) big brown bats.

**Table 5.** Mean ( $\pm$  SE) of 11 landscape-scale variables at mist netting capture and non-capture sites for bat species (*Myotis yumanensis*, *M. californicus*, *M. evotis*, *M. thysanodes*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Antrozous pallidus*, *Lasiurus borealis*, and *Lasiurus cinereus*) in Whiskeytown National Recreation Area, California, USA, 2002 and 2003 ( $n$  = no. of sample sites).

Variable	All bat species				Yuma myotis				Silver-haired bats				Big brown bats			
	Captured $n = 35$		Not captured $n = 12$		Captured $n = 18$		Not captured $n = 29$		Captured $n = 18$		Not captured $n = 29$		Captured $n = 12$		Not captured $n = 35$	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Total edge	45,700	1,420 <sup>a</sup>	34,900	3,150	46,600	1,780	40,800	2,050	46,100	1,880	41,000	2,040	45,500	2,340	42,100	1,810
Patch richness	5.1	0.2	4.3	0.5	5.5	0.3 <sup>a</sup>	4.4	0.3	5.3	0.3	4.6	0.3	5.0	0.3	4.9	0.3
$\bar{x}$ summer temp	19.1	0.4	16.7	1.1	19.8	0.2	17.6	0.6	19.5	0.4	17.8	0.6	18.8	0.6	18.3	0.5
Total summer precipitation	2.5	0.02 <sup>a</sup>	2.7	0.1	2.5	0.01	2.6	0.1	2.5	0.02 <sup>a</sup>	2.6	0.05	2.5	0.04	2.6	0.04
Riparian flyways	7,590	778	4,700	807	7,670	1,140	6,350	755	9,160	1,050 <sup>a</sup>	5,420	691	7,730	1,280	6,550	741
Terrestrial flyways	26,900	2,430 <sup>a</sup>	16,700	2,290	28,600	3,223	21,600	2,470	29,700	3,870	20,900	2,000	29,200	4,820	22,600	2,090
Distance to nearest stream	115	41.1	98.3	56.9	98.8	43.5	118	47.8	57.2	22.0	144	52.2	2.5	2.5 <sup>a</sup>	148	43.5
Distance to nearest lake or pond	1,420	281 <sup>a</sup>	2,970	765	785	204 <sup>a</sup>	2,450	429	1,170	292	2,210	437	1,350	314	1,970	385
Canopy closure	0.48	0.06	0.57	0.11	0.35	0.08 <sup>a</sup>	0.59	0.07	0.42	0.08	0.55	0.07	0.65	0.08	0.45	0.07
Tree size	39.6	3.4	42.1	5.4	39.2	5.1	40.9	3.4	41.5	5.2	39.4	3.4	41.6	4.6	39.8	3.5
Elevation	468	42.0 <sup>a</sup>	791	143	380	19.2 <sup>a</sup>	655	76.6	382	23.4 <sup>a</sup>	655	76.3	419	37.8	595	66.4

<sup>a</sup> Means are significantly different ( $P < 0.05$ ).

<400 m (Fig. 1). A posteriori analyses showed mean differences at capture and non-capture sites for 3 variables were significant: elevation ( $P = 0.002$ ), riparian flyways ( $P = 0.005$ ), and total summer precipitation ( $P = 0.044$ ; Table 5).

The model that contained only elevation was best fitting for big brown bats, although all models had similar classification accuracies (Table 2). Unconditional sampling variance for the elevation coefficient was 0.2 (Table 3). Elevation provided the highest relative importance for big brown bats (Table 4). The odds of capturing a big brown bat decreased 0.4 when elevation increased by 400 m (Table 3). The most parsimonious model predicted that the highest probability (10–40%) of capturing a big brown bat was in areas with elevations <900 m (Fig. 1). A posteriori analysis showed mean differences at big brown bat capture and non-capture sites for elevation were significant ( $P = 0.010$ ; Table 5).

## DISCUSSION

Modeling indicated that total edge was a landscape-scale variable that influenced the distribution of all species combined. Studies have suggested that many species use linear landscape elements for successful foraging or commuting (Grindal 1996, Krusic et al. 1996, Russo et al. 2002, Patriquin and Barclay 2003), echo-orientation (Verboom et al. 1999), and protection from predators or wind (Verboom and Huitema 1997, Verboom 1998).

Proximity to lakes and ponds was important in predicting the occurrence of Yuma myotis. Yuma myotis are associated with streams, rivers, ponds, or lakes (Whitaker et al. 1977, Zeiner et al. 1990) and are more closely associated with water than any other North American species (Verts and Carraway 1998). Additionally, Brigham et al. (1992) reported that in Canada, Yuma myotis spent more time over water than in other habitats.

Elevation was an important factor influencing silver-haired bat distribution and was the only variable in the most parsimonious model. Almost all silver-haired bat captures were at low-elevation sites close to the reservoir. In contrast, most unsuccessful capture sites were high-elevation sites away from the reservoir where reduced opportunities for drinking water, and possibly foraging, likely existed. Model selection uncertainty was highest for silver-haired bats (4 of 7 models  $AIC_c < 2$ ); thus, researchers should interpret this model set with caution. Our second best model, which contained the variables elevation and riparian flyways, had a very low  $AIC_c$  difference. Researchers should consider this model as a suitable model alternative to the elevation model because poor urine-concentrating ability probably restricts silver-haired bats to mesic habitats (Geluso 1978, Zeiner 1990). Because several authors have reported that silver-haired bats often use mature forest stands that provide exfoliating bark and snags for roosting (Perkins and Cross 1988, Thomas 1988), we expected that tree size would have been more important in modeling this species' distribution. However, tree size had the lowest relative importance for silver-haired bats of all variables in the global model.

Perhaps our findings differ from the literature, which describes roost-site habitat, because we captured bats at foraging and drinking sites, which can be some distance from roost trees. Additionally, because of historical logging, few mature stands exist in WHIS.

Elevation was an important variable in modeling big brown bat distribution; however, we had difficulty predicting big brown bat absence. This may result from the fact that big brown bats are habitat generalists and are widespread. Low elevations in WHIS have a higher abundance of aquatic habitats for foraging than do similar high-elevation habitats. In some areas, big brown bats use aquatic habitats as focal points for foraging (Hayes 2003), and Bell (1980) reported big brown bat activity throughout the night in riparian forests to be 7.4 times higher than in juniper and 11.9 times higher than in desert habitats. Thus, we could expect big brown bats to occur at low elevations more frequently in WHIS. Additionally, in topographically diverse regions, Cryan et al. (2000) found foraging activity by reproductive females to be greater at lower elevations where insect densities are higher. Of our big brown bat captures, 91.7% were females, 59.6% of which were reproductively active. Perhaps big brown bats are commuting to lower elevations to exploit foraging areas that are more profitable because there are likely to be greater insect abundances in these habitats due to warmer ambient air temperatures.

Cryan et al. (2000) and others (Allen 1939, Fenton et al. 1980, Grindal et al. 1999) have reported elevational differences in distribution among sexes of insectivorous bats. Lower-elevation habitats may improve both foraging and thermoregulatory efficiencies of reproductive females. Due to low sample sizes, we were unable to split out sexes of bats for distribution modeling. Our models represent species distributions at WHIS and may be similar to other low-elevation habitats where females are more abundant, but readers should not apply our models to high-elevation habitats where different proportions of males and females may exist. At high elevations, species distributions may be responding to different variables at the landscape scale (Duff 2004).

Our analytical approach assumes that capture probability of species in different areas are a function of their presence, rather than artificial processes, such as the methodology used to collect data. Many factors could have affected our capture probabilities (e.g., no. of mist nets deployed, time spent at each site, weather variability, and site selection). We attempted to minimize these artificial processes in several ways. We visited sites several times when possible and closed mist nets when weather (wind or rain) warranted. Whiskeytown National Recreation Area has an equable summer climate, with little rain in the summer (on only one occasion did rain affect our sampling efforts) and warm temperatures throughout the summer season ( $\bar{x}$  temp [ $^{\circ}$  C] and SE at the time mist nets were opened and closed were 25.4 [0.75] and 18.8 [0.44], respectively). We sampled a variety of sites (aquatic and terrestrial) to ensure we distributed our samples

spatially across the study area, stratifying by habitat and elevation. At terrestrial sites, we made every effort to increase capture probabilities (we placed nets in areas with multiple corridors for bat use [road and trail intersections], with overhanging vegetation that funneled bats into our nets). At road and trail sites, we placed two of the same-sized nets together, one raised above the other.

Where model sets show ambivalence, readers should interpret our predictive maps with caution. Models with high ambivalence suggest that none of the models within a model set were particularly better than the others in predicting bat occurrence. Thus, some of our models had high model selection uncertainty for our model sets (Burnham and Anderson 2002). We did not use acoustic sampling methods during this study, but we believe augmenting mist net surveys with acoustic surveys may lower model uncertainty and increase predictive power. Our results are applicable exclusively to foraging habitats for bats because we used only mist netting during the study, not acoustical sampling or radiotelemetry techniques. For this reason, resource managers must exercise great care when making management decisions based upon our models. Misinterpretation will result if managers apply model results beyond foraging habitats for which we designed the models because areas of low occurrence may actually contain critical roosting habitat.

We believe that other, more direct factors exist (e.g., local-scale habitat quality, prey availability, roosting habitat) that have a stronger influence on bat distributions than those we used. We recommend investigating this aspect of predicting bat distributions. Additionally, model uncertainty and low predictive power could be due to noise in our mist net data (night-to-night weather variability, species frequently switching roosts, poor netting success for certain high-flying species), or in the GIS layers (GPS or classification inaccuracies). Furthermore, spatial scale of data and sample landscape used in metrics (radius = 1,500 m) for this study may not be appropriate for some bats we modeled.

## MANAGEMENT IMPLICATIONS

Based upon our modeling results, we present the following recommendations for future mist netting survey efforts. For all bat species combined, managers should use areas in WHIS with high total edge to predict locations where bats will be foraging. Our findings indicate that managers could effectively sample Yuma myotis proximal to lakes and ponds, and they could sample silver-haired and big brown bats at low-elevation habitats. These locations are important foraging habitats for bat species in WHIS, and managers should focus future mist netting efforts in these habitats. By following these guidelines, we believe managers may conduct future sampling efforts efficiently and within financial and logistical constraints.

## ACKNOWLEDGMENTS

We thank E. Arnett, J. Hayes, and 3 anonymous reviewers for comments on this manuscript. We also thank L.

Johannes and S. Tatnall for field assistance and P. Duprey, D. Sarr, and R. Weatherbee for providing logistical support. We are particularly thankful for statistical advice provided by to T. Edwards, J. Jones, and W. Thompson. The National Park Service Inventory and Monitoring Program, Ball State University, and the National Fish and Wildlife Foundation provided funding for this study.

## LITERATURE CITED

- Allen, G. M. 1939. Bats. Dover Publications, New York, New York, USA.
- Allison, P. D. 1999. Logistic regression using the SAS System, theory and application. SAS Institute, Cary, North Carolina, USA.
- Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* 33:339–347.
- Bell, G. P. 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology* 58:1876–1883.
- Brigham, R. M., H. D. J. N. Aldridge, and R. L. Mackey. 1992. Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. *Journal of Mammalogy* 73:640–645.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- California Vegetation [CALVEG]. 2002 Oct 25. USFS California Land Cover Mapping and Monitoring Program vegetation data, CALVEG home page. <<http://frap.cdf.ca.gov/data/frapgisdata/select.asp>>. Accessed 25 Oct 2002.
- Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy* 81:719–725.
- DAYMET. 2003 Sep 18. Daymet climatological summaries for the conterminous United States 1980–1997. University of Montana, Numerical Terradynamic Simulation Group Daymet home page. <<http://www.daymet.org>>. Accessed 18 Sep 2003.
- Duff, A. A. 2004. Predicting bat occurrence in northern California using landscape-scale variables. Thesis, Ball State University, Muncie, Indiana, USA.
- Fenton, M. B., C. G. Van Zyll De Jong, G. P. Bell, D. B. Campbell, and M. Laplante. 1980. Distribution, parturition dates, and feeding of bats in south-central British Columbia. *Canadian Field-Naturalist* 94:416–420.
- Fleishman, E., R. Mac Nally, J. P. Fay, and D. D. Murphey. 2001. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. *Conservation Biology* 15:1674–1685.
- Gabler, K. I., J. W. Laundre, and L. T. Heady. 2000. Predicting the suitability of habitat in southeast Idaho for pygmy rabbits. *Journal of Wildlife Management* 64:759–764.
- Geluso, K. N. 1978. Urine concentrating ability and renal structure of insectivorous bats. *Journal of Mammalogy* 59:312–323.
- Grindal, S. D. 1996. Habitat use by bats in fragmented forests. Pages 260–272 in R. M. R. Barclay and R. M. Brigham, editors. Proceedings of bats and forests symposium, 19–21 October 1995, Victoria, British Columbia, Canada. Resources Branch, Ministry of Forests Work Paper 23/1996, Victoria, British Columbia, Canada.
- Grindal, S. D., J. L. Morissette, and R. M. Brigham. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Canadian Journal of Zoology* 77:972–977.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hayes, J. P. 2003. Habitat ecology and conservation of bats in western coniferous forests. Pages 81–119 in C. J. Zabel and R. G. Anthony, editors. Mammal community dynamics in coniferous forests of western North America: management and conservation. Cambridge University Press, Cambridge, United Kingdom.
- Jaberg, C., and A. Guisan. 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology* 38:1169–1181.
- KLMNGIS. 2002. Version 1. Klamath Network Inventory and Monitoring Program. National Park Service, Ashland, Oregon, USA.
- Krusic, R. A., M. Yamasaki, C. D. Neefus, and P. J. Pekins. 1996. Bat habitat use in White Mountain National Forest. *Journal of Wildlife Management* 60:625–631.
- Manel, S., J. M. Dias, S. T. Buckton, and S. J. Ormerod. 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *Journal of Applied Ecology* 36:734–747.
- MapMart Interactive Data Warehouse. 2002. United States Geologic Survey 10 and 30 m digital elevation models. <<http://www.mapmart.org>>. Accessed 12 Oct 2002.
- Morrell, T. E., and A. A. Duff. 2005. Distribution and relative abundance of bats in Whiskeytown National Recreation Area, Lassen Volcanic National Park, and Lassen National Forest: with emphasis on predicting bat occurrence using landscape scale characteristics, final report 2005. Ball State University Department of Biology Technical Report 4, Muncie, Indiana, USA.
- Morrell, T. E., M. J. Rabe, H. Green, J. C. deVos, and C. R. Miller. 1999. Bats captured in two ponderosa pine habitats in north central Arizona. *Southwest Naturalist* 44:501–506.
- Nicolas, R., A. Lehmann, and P. Joly. 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. *Biodiversity and Conservation* 11:2143–2165.
- O’Shea, T. J., and M. A. Bogan, editors. 2003. Monitoring trends in bat populations of the United States and territories: problems and prospects. U.S. Geological Survey Information and Technology Report USGS/BRD/ITR 2003–0003, Fort Collins, Colorado, USA.
- Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology* 40: 646–657.
- Perkins, J. M., and S. P. Cross. 1988. Differential use of some coniferous forest habitats by hoary and silver-haired bats in Oregon. *Murrelet* 69: 21–24.
- Russo, D., G. Jones, and A. Migliozzi. 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. *Biological Conservation* 107:71–81.
- Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* 52:619–626.
- Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190:214–251.
- Verboom, B. 1998. The use of edge habitats by commuting and foraging bats. DLO Institute for Forestry and Nature Research (IBN-DLO), Wageningen, the Netherlands.
- Verboom, B., A. M. Boonman, and H. J. G. A. Limpens. 1999. Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). *Journal of Zoology* 248:59–66.
- Verboom, B., and H. Huitema. 1997. The importance to linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12:117–125.
- Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley and Los Angeles, USA.
- Western Regional Climate Center. 1999 Mar 30. Monthly average temperature and precipitation, Whiskeytown Dam, California. <[www.wrcc.dri.edu](http://www.wrcc.dri.edu)>. Accessed 30 Mar 2005.
- Whitaker, J. O., Jr., C. Maser, and L. E. Keller. 1977. Food habits of bats of western Oregon. *Northwest Science* 51:46–55.
- Zeiner, D. C., W. F. Laudenslayer, Jr., K. E. Mayer, and M. White, editors. 1990. California’s wildlife. Volume 3: mammals. California statewide wildlife habitat relationships system. The Resources Agency, Department of Fish and Game, Sacramento, California, USA.

Associate Editor: Kuenzi.