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Habitat Use by Saw-Whet Owls in the Sierra Nevada

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ABSTRACT Northern saw-whet owls (*Aegolius acadicus*) are secondary cavity-nesters and their dependence on snags has potential repercussions on forest management practices. Descriptive studies exist regarding habitat characteristics around saw-whet nest and roost areas, yet few studies have examined associations within larger areas or relative to snag characteristics (e.g., density). We conducted owl broadcast surveys and snag sampling during the spring and summer of 2006 and 2007 in the Lake Tahoe Basin of the central Sierra Nevada; we measured additional habitat variables from Geographic Information System layers. We modeled detection and occupancy probabilities for saw-whets using sampling and site covariates at survey sites. In addition, we used stepwise logistic regression to compare habitat characteristics at owl use sites and nonuse sites at 2 spatial scales. Detection probability was low in 2006 and decreased throughout the survey period; detection probability was slightly higher in 2007 and unaffected by day of survey. Probability of occupancy was affected by elevation and dominant tree species in 2007. Similarly, stepwise logistic regression indicated saw-whet occurrence was negatively correlated with the percentage of area dominated by white fir (*Abies concolor*) at both the macrohabitat (approx. 260 ha) and microhabitat (approx. 20 ha) scales and was positively correlated with the percentage of area containing open canopy at the microhabitat scale. We did not find correlations between saw-whet occurrence and snag characteristics. Current restoration projects in areas of the Sierra Nevada aim to decrease relative abundance of white fir and the number of snags in forest stands. We recommend continued monitoring of saw-whets to understand potential effects of these restoration activities. Our estimates of saw-whet occupancy and detection probabilities can be used by forest managers to determine necessary survey effort for reliable results when developing monitoring protocols.

KEY WORDS *Aegolius acadicus*, detection probability, Lake Tahoe Basin, logistic regression, occupancy, PRESENCE, secondary cavity nester, snags, spatial scale.

Impacts of human activities on forest-dwelling wildlife populations in the United States have been the focus of numerous studies over the past several decades (e.g., Soutiere 1979, Wisdom and Bates 2008). In the Sierra Nevada of California, USA, human activities have included logging, livestock grazing, development, recreation, and fire suppression, resulting in alteration of the vegetation composition and structure of many forest stands (Beesley 1996, Manley et al. 2000). Owls are a large portion of the top avian predators in the Sierra Nevada and potential effects of human activities on owl populations are not well understood (e.g., Johnsgard 2002). Researchers must begin with a thorough examination of owl–habitat associations to understand how human activities, including forest management practices, could influence owl distributions.

Several owl species known to occur in higher elevations (>1,800 m) of the central Sierra Nevada are small (<200 g), secondary cavity-nesters: the flammulated owl (*Otus flammeolus*), northern pygmy-owl (*Glaucidium gnoma*), northern saw-whet owl (*Aegolius acadicus*), and western screech-owl (*Megascops kennicottii*; Orr and Moffitt 1971, Schlesinger and Romsos 2000). These 4 owl species typically nest in naturally formed tree cavities or in cavities excavated by other avian species (Johnsgard 2002). Nesting cavities are often located in standing dead trees, known as snags. Density and distribution of snags are one component of forest structure and are the focus of much research and debate that aims to shape forest management guidelines (Raphael and White 1984, Ganey and Vojta 2004, Hutto

2006). Logging and fire suppression can affect snag density and distribution and, thus, may affect the species that depend on snags for nesting, roosting, or foraging (Covington et al. 1994). Researchers have typically focused on fine-scale relationships between owls and nest or roost sites or have focused on broad-scale relationships with vegetation types in their study area; few researchers have examined owl–habitat relationships at multiple spatial scales (although see Hayward and Garton 1988, Ripple et al. 1997). Examining the owl's habitat at a range of scales within one study may result in a comprehensive understanding of the owl's needs, from the microhabitat (corresponding to needs of an individual) to the macrohabitat (corresponding to distribution and abundance of populations; Block and Brennan 1993).

Occupancy modeling allows for estimation of occupancy and detection probabilities while including covariates such as habitat characteristics (MacKenzie et al. 2006). Recent research emphasizes the need to incorporate detection probability in studies of species occupancy and habitat use to avoid the biases inherent in index-based approaches (e.g., MacKenzie et al. 2002, Tyre et al. 2003). Species may be present at a site but remain undetected during surveys, leading to potentially erroneous conclusions of habitat use (MacKenzie et al. 2006). Estimating detection probability also provides information on efficacy of a study design and survey effort needed in future surveys (MacKenzie and Royle 2005).

Our goal was to increase understanding of northern saw-whet owls in the central Sierra Nevada by examining their distributions and habitat associations at both a broad and fine scale. The United States Forest Service Lake Tahoe

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Basin Management Unit (LTBMU) initiated multispecies owl surveys in 2004 in areas of restoration concern in several watersheds of the Lake Tahoe Basin (LTB). Although we maintained the multispecies surveys, we focused our current analysis on the northern saw-whet owl (hereafter, saw-whet) because we rarely detected the other small owl species during surveys. Our objectives were to 1) document northern saw-whet owl distribution based on nocturnal broadcast surveys, 2) estimate probabilities of detection and occupancy of the species, 3) examine the relationship between habitat characteristics and owl occurrence at both broad and fine scales, and 4) provide information for future monitoring of saw-whet owls in the central Sierra Nevada.

STUDY AREA

Our study area was the LTB, which straddles the border of California and Nevada, USA, in east-central Sierra Nevada (Fig. 1). The LTB covers approximately 1,300 km², nearly 500 km² of which is the lake itself, with elevations of 1,900–3,315 m (Elliott-Fisk et al. 1997). Monthly average temperatures ranged from −7.6° C to 25.7° C throughout the year (Western Regional Climate Center [WRCC] 2008). Nightly temperatures during our nocturnal surveys ranged from −2.5° C to 20.0° C for May–July 2006 and −10.0° C to 14.0° C for March–June 2007. Average annual precipitation in the region was 80 cm with most falling as snow during winter (Manley et al. 2000, WRCC 2008). Total precipitation during the 2006 and 2007 field seasons was below average: 1.4 cm for May–July 2006 and 8.6 cm for March–June 2007 versus a long-term (100-yr) average of 5.4 cm for May–July and 20.5 cm for March–June (WRCC 2008).

The LTB changed considerably in the past 150 years due to logging, livestock grazing, fire suppression, development, and tourism (Elliott-Fisk et al. 1997, Lindström 2000). Many forest stands contained higher tree densities and smaller trees due to logging in the 1800s and fire suppression in the last century (Manley et al. 2000, Taylor 2007). Tree species composition shifted from mostly pine (*Pinus* spp.) and other fire-tolerant species to fire-intolerant firs (*Abies* spp.; Manley et al. 2000). Approximately 1,700 km of state highways, national forest roads, and private roads, along with hundreds of kilometers of hiking trails, increased human access into forest stands. The LTBMU managed 80% of the land in the LTB (LTBMU 2008).

Manley et al. (2000) described 3 main vegetation zones in the LTB. The lower montane zone (<2,200 m) was comprised mainly of Jeffrey pine (*Pinus jeffreyi*) forests, white fir (*Abies concolor*) forests, and mixed-conifer forests (i.e., white fir, Jeffrey pine, and lodgepole pine [*Pinus contorta*]). The upper montane zone (2,200–2,600 m) contained forest types dominated by red fir (*Abies magnifica*) and had less shrub and herbaceous cover than lower elevations. The subalpine zone (>2,600 m) contained mainly mixed subalpine woodlands of mountain hemlock (*Tsuga mertensiana*), whitebark pine (*P. albicaulis*), and smaller proportions of red fir, lodgepole pine, and western white pine (*P. monticola*). Wet and dry meadows, quaking
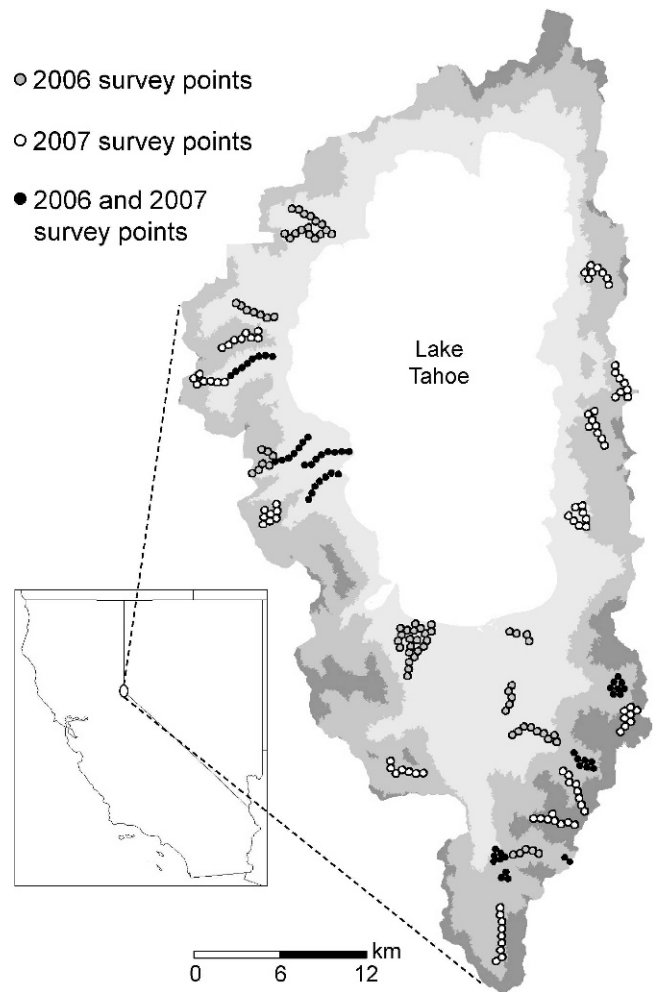

Figure 1. Map of the Lake Tahoe Basin, relative to the states of California and Nevada, USA, and areas surveyed for 6 owl species during May–July 2006 and March–June 2007 nocturnal broadcast surveys. Shading of the basin indicates 3 elevation ranges: <2,200 m, 2,200–2,600 m, and >2,600 m, with the lightest shade corresponding to the lowest elevations.

aspen (*Populus tremuloides*) groves, and riparian areas were scattered throughout the LTB.

METHODS

Broadcast Surveys

We surveyed 32 groups of 2–9 points throughout the LTB. Grouping points allowed us to survey more points each night because we walked between points. Points were 500 m apart to maintain spatial independence, that is, to avoid detecting the same individual owl at multiple survey points. Because we were dealing with multiple owl species, we based the 500-m distance in part on home range size estimates of the smaller owl species (Cannings 1987, Reynolds and Linkhart 1987, Hayward and Garton 1988, Holt and Petersen 2000, Hinam and St. Clair 2008). Although on the smaller side of these home range values, we felt 500 m was an adequate spacing between points given the wide range of possible home range sizes and the area that we could effectively cover in one night on foot.

We surveyed in forested lands from approximately 1,900-m to 2,900-m elevation. We established half the groups of

points in areas of restoration interest to the LTBMU and randomly distributed the remaining groups throughout the basin (see Groce 2008). We randomly placed survey points within these groups using ArcMAP 9.2 but constrained points by 1) maintaining 500-m spacing between points in a group; 2) avoiding sections of steep, unsafe slopes; and 3) remaining within United States Forest Service (USFS) boundaries.

At each survey point and using nocturnal broadcast surveys, we surveyed for 6 owl species: flammulated owl, northern pygmy-owl, northern saw-whet owl, western screech-owl, long-eared owl (*Asio otus*), and great horned owl (*Bubo virginianus*). We included long-eared owl and great horned owl calls to document locations of these potential predators. We did not include California spotted owls (*Strix occidentalis occidentalis*) because the LTBMU maintained a separate project focused on this species. Broadcast surveys consisted of projecting owl calls through an amplified speaker from specified points (hereafter survey points) to induce an owl to respond. Numerous studies have shown broadcast surveys to be effective for cryptic or nocturnal species (e.g., Johnson et al. 1981, Bosakowski and Smith 1998). We used a portable compact disc player and Foxpro Wildlife Caller® (FOXPRO Inc., Lewiston, PA) to broadcast owl calls. We broadcast calls in order of smallest to largest species to avoid possible intimidation of smaller species (Fuller and Mosher 1981, Hayward and Garton 1988). We used standard owl calls from Peterson Field Guides Series® (Houghton Mifflin, New York, NY) and *Stokes Field Guide to Bird Songs*® (Hachette Audio, New York, NY). We set the volume of the broadcasting unit to a level barely audible to the surveyor at an unobstructed distance of 250 m; thus, each survey point effectively covered approximately 20 ha (i.e., 250-m-radius circle).

We surveyed from mid-May through July 2006 and mid-March through mid-June 2007. Peak calling periods for smaller owl species ranges mid-February through mid-June, depending on location (e.g., CO: Palmer 1987; the Appalachians: Milling et al. 1997; MT: Takats et al. 2001; Sierra Nevada: Crozier et al. 2003). We surveyed each point 3 or 6 times to determine both distribution of and detection probability for the saw-whet owl. Six surveys provided us more precise estimates of detection probabilities, whereas surveying some points 3 times enabled us to survey more points throughout the LTB. We began each survey 15 minutes after sunset and continued through the night until we completed all survey points in a site. We randomized the order of survey points for each visit to limit effects of temporal bias (Morrison et al. 2008). We remained at each survey point for 22 minutes and alternated between broadcasting owl calls and periods of silence (see Groce 2008). We recorded species and direction and distance of each detected owl response. We estimated and categorized distances as follows: 0–10 m, 10–50 m, 50–100 m, 100–200 m, and >200 m. When possible, we triangulated on the owl to increase accuracy of its estimated location or we located the tree from which the owl called.

We did not survey during heavy rain, wet snow, or in winds >20 km/hr.

Habitat Use

We plotted the locations of all owls detected in 2006 and 2007 using ArcMAP. We inferred that presence of an owl indicated use of an area; that is, individuals were using resources to meet survival needs (e.g., foraging, nesting; Block and Brennan 1993). We defined macrohabitat by first creating a 500-m buffer around each survey point. We merged buffers of adjacent survey points where owls were detected into owl use sites and merged buffers of adjacent points with no owl detections into nonuse sites. Average size of each macrohabitat site was 260 ha (range = 92–460 ha) and was large enough to encompass several potential saw-whet owl territories (Cannings 1987, Hinam and St. Clair 2008). We measured vegetation characteristics (e.g., canopy cover and dominant tree species cover) within each macrohabitat site from a Geographic Information System (GIS) layer that included vector format vegetation information specific to the LTB (Dobrowski et al. 2005). Canopy cover categories included closed canopy (>60% tree cover), open canopy (primarily 25–60% cover), shrubland (shrub dominated, 10–25% tree cover), herbaceous (herb dominated, primarily 1–10% tree cover), sparse vegetation (primarily <1% tree cover), and non-vegetated. We calculated the proportion of area covered by different canopy categories and dominant tree species within each site. We focused on canopy cover and tree species at the macrohabitat scale because vegetation classes and species composition may be informative in predicting saw-whet occurrence (e.g., Simpson 1972, Cannings 1993).

We created 250-m buffers around each saw-whet location in ArcMAP to define the scale of the microhabitat (approx. 20 ha) and limit overlap with adjacent points. As noted earlier, 20 ha is on the smaller end of saw-whet home range size; without knowing the actual size or location of each owl's territory, 20 ha seemed a reasonable size within which to obtain a general sense of habitat associations in an area larger than a nest or roost site. We considered each owl location to be a separate sample at the microhabitat scale and assumed owl locations indicated use of the area. We also created 250-m buffers around randomly selected survey points where we did not detect saw-whets in either year (i.e., nonuse sites) and assumed these areas were not used by owls. Again using the GIS vegetation layer, along with GIS layers of digital elevation models and waterways, we estimated elevation, distances to closest forest openings and streams, and the proportion of canopy and tree species cover within the buffered area of each use and nonuse point (Palmer 1986, Hayward and Garton 1988, Cannings 1993, Anderson and Clark 2002).

We measured snag characteristics in the field for all snags we found in 6 60 × 40-m plots arrayed within each of 40 use and 40 nonuse microhabitat sites, because snag information was not available on the GIS layers. Researchers acknowledge snags as an important component of the owl's habitat for providing nest cavities, yet few studies have

examined the relationship between snag characteristics (e.g., density, size) and owl presence at scales greater than that of the immediate nest area (Johnson and Anderson 2003). We determined the number of microhabitat sites to survey for snags, and the number and size of plots within sites, by sample size and power analyses as described by Groce (2008). Within each plot we counted and measured every snag, defined as standing dead trees $\geq 45°$ from horizontal, ≥ 13 cm diameter at breast height, and ≥ 1.5 m in height. Snag measurements included diameter at breast height, height, decay class (i.e., extent of snag decay), number of cavities, and tree species. We visually estimated decay class on a scale of 1 to 5, with 1 indicating a tree that recently died and was relatively intact and 5 indicating a snag in an advanced state of decay (Manley and McIntyre 2004). We did not climb snags and were therefore unable to verify utility of all cavities we counted. We assessed ground cover in the same plots as snag surveys. We used the point intercept method along the centerline of each plot and calculated percent cover of open (e.g., bare ground, leaf litter) versus covered ground (e.g., shrubs, logs, herbaceous vegetation).

Statistical Analyses

We used PRESENCE 2.2 (Hines 2006) to estimate probabilities of detection (p) and occupancy (ψ) for 132 survey sites in 2006 and 128 survey sites in 2007. Program PRESENCE allowed for incorporation of missing observations (treated as no information with regard to detection or nondetection [MacKenzie et al. 2002]), which enabled us to combine data from the 3-visit and 6-visit surveys. If we suspected that we detected the same owl at 2 adjacent survey points (a violation of the assumption of spatial independence), we removed 1 of the 2 survey points from the data set prior to analysis. Program PRESENCE evaluates factors that may influence detection or occupancy of a site, which we defined as a 250-m-radius circle around a survey point. For all points surveyed, sampling covariates (i.e., factors that may affect detection probability) included time of season, whereas site covariates (i.e., factors that may influence species occupancy) included elevation and dominant tree species. We examined time of season in 2 ways: number of days or number of 2.5-week periods since start of surveys (where 2.5 weeks approximated time needed to complete a round of surveys at all sites). We treated dominant tree species (i.e., white fir, red fir, Jeffrey pine, or mixed species) as a categorical covariate and used elevation as a continuous variable. We also examined the interaction between dominant tree species and elevation. We estimated separate detection probabilities and occupancy rates for 2006 and 2007 due to differences in survey periods between years. We ranked models using Akaike's Information Criterion (AIC) in an information-theoretic framework (Burnham and Anderson 1998).

Independent of the PRESENCE analysis, we used stepwise logistic regression to examine characteristics around owl locations, which differed from survey point locations by 10–200 m. We used SPSS 14.0 (SPSS Inc.,

Chicago, IL) for statistical analyses of macrohabitat and microhabitat variables. Given the dichotomy of the dependent variable (i.e., detection or no detection), we used forward stepwise logistic regression to determine which variables were correlated with saw-whet owl occurrence at each spatial scale. Due to a lack of information on habitat associations of saw-whet owls in the Sierra Nevada, we intended our habitat analysis to be exploratory and a basis from which future hypotheses and model testing could be developed; thus, we neither developed nor tested a priori hypotheses.

We used Mann–Whitney U tests for univariate analyses to compare variables between use and nonuse sites. We then included variables that differed ($P \leq 0.15$) in forward stepwise logistic regression to potentially develop a multivariate model estimating probability of saw-whet occupancy, and thus use, of a site. We used forward selections with $\alpha = 0.10$ for a variable to be included or removed from the model (Pearce and Ferrier 2000). We assessed overall fit of the final model using Hosmer–Lemeshow goodness-of-fit test and calculated classification accuracy (i.e., ability of the model to correctly predict saw-whet use or nonuse). We conducted a separate t-test to determine how snag densities varied between areas dominated by white fir and areas dominated by either red fir or Jeffrey pine, regardless of owl occurrence.

RESULTS

We surveyed 226 points in the LTB, 56 of which we surveyed both years (Fig. 1). We conducted 3 and 6 surveys at 55 and 77 points, respectively, in 2006; in 2007, we conducted 3 and 6 surveys at 92 and 58 points, respectively. We detected 14 saw-whets in 2006 and 38 saw-whets in 2007 during nocturnal broadcast surveys. There were spatial and temporal differences between years; in general, surveys in 2007 occurred earlier in the season and at a wider range of elevations than in 2006. For 2006, model results indicated strong evidence of a seasonal effect on detectability (Table 1). Although detection probabilities were highest at the start of the survey period (mid-May), they remained low (<0.20) throughout the season for both top-ranked models and decreased to nearly zero by the last round of surveys (Fig. 2). Estimated occupancy for the top-ranked model, which included the sampling covariate of 2.5-week survey periods, was moderate ($\psi = 0.33$, SE = 0.20). However, when detection probabilities are low (i.e., $p \leq 0.15$), occupancy estimates are unreliable and may be biased high (MacKenzie et al. 2002, Bailey et al. 2004). Models that included site covariates of elevation or dominant tree species were not supported relative to models that included sampling covariates in 2006. Surveys began 2 months earlier in 2007 (mid-Mar), a more appropriate sampling season given the breeding biology of the species (e.g., Crozier et al. 2003). For 2007, most models that contained sampling covariates were the least supported. Instead, site covariates of elevation and dominant tree species were included in top-ranked models (Table 1). The top-ranked models had higher detection probabilities in 2007 ($p = 0.28$, SE =

Table 1. Model selection results based on Akaike's Information Criterion (AIC) for estimating probability of detection (p) and occupancy (ψ) of northern saw-whet owls in the Sierra Nevada, California and Nevada, USA, 2006–2007. Sampling covariates included day since start of surveys (Day) and every 2.5 weeks since start of surveys (2.5Wk). Site covariates included dominant tree species (TreeSp) and elevation in meters/1,000 (Elev).

Model	AIC	ΔAIC[a]	AIC wt[b]	Model likelihood	No. of parameters	$-2 \times$ LogLike[c]
2006 surveys						
$\psi(.)p(2.5\text{Wk})$	151.47	0.00	0.5887	1.0000	3	145.47
$\psi(.)p(\text{Day})$	152.42	0.95	0.3661	0.6219	3	146.42
$\psi(.)p(.)$	158.85	7.38	0.0147	0.0250	2	154.85
$\psi(\text{TreeSp})p(.)$	158.99	7.52	0.0137	0.0233	5	148.99
$\psi(\text{Elev,TreeSp})p(.)$	159.56	8.09	0.0103	0.0175	6	147.56
$\psi(\text{Elev})p(.)$	160.47	9.00	0.0065	0.0111	3	154.47
2007 surveys						
$\psi(\text{Elev})p(.)$	353.36	0.00	0.3853	1.0000	3	347.36
$\psi(\text{Elev,TreeSp})p(.)$	353.76	0.40	0.3154	0.8187	6	341.76
$\psi(\text{Elev})p(2.5\text{Wk})$	355.35	1.99	0.1424	0.3697	4	347.35
$\psi(\text{TreeSp})p(.)$	357.52	4.16	0.0481	0.1249	5	347.52
$\psi(.)p(.)$	358.27	4.91	0.0331	0.0859	2	354.27
$\psi(\text{Elev} \times \text{TreeSp})p(.)$	358.28	4.92	0.0329	0.0854	9	340.28
$\psi(\text{TreeSp})p(2.5\text{Wk})$	359.51	6.15	0.0178	0.0462	6	347.51
$\psi(.)p(2.5\text{Wk})$	360.18	6.82	0.0127	0.0330	3	354.18
$\psi(.)p(\text{Day})$	360.27	6.91	0.0122	0.0316	3	354.27

[a] ΔAIC is the difference in AIC values between each model and the lowest AIC model.
[b] AIC wt is the model weight.
[c] Twice the negative log-likelihood.

0.04) than in 2006 and indicated that elevation and dominant tree species influenced saw-whet occupancy (Fig. 3).

We examined 25 saw-whet use sites and 9 nonuse sites at the macrohabitat scale. Of the 7 variables we examined, univariate analyses indicated sites used by saw-whets contained, on average, 3 times more red fir (% cover, $P = 0.030$) and 3 times less white fir (% cover, $P = 0.041$) than nonuse sites (Table 2). Forward stepwise procedures resulted in a single-variable model, indicating percentage of area dominated by white fir was negatively correlated with saw-whet occurrence (Table 3; Fig. 4a). Results suggested that for a 1% increase in percentage of white fir cover there was an approximate 2.4% decrease in the odds of the site being occupied by a saw-whet (odds = 0.976). The model fit the data moderately well with a Hosmer–Lemeshow value of 0.304 and correctly predicted saw-whet use at 76.5% of sites with sensitivity and specificity of 88 and 44%, respectively (Table 3).

We examined 40–52 use and 40 nonuse sites at the microhabitat scale; sample sizes differed depending on methods we employed to measure variables (i.e., in-field vs. GIS data; Table 2). Univariate analyses indicated several variables were significant ($P \leq 0.15$). Elevation, percentage of area classified as open canopy, percentage of area dominated by either lodgepole pine or red fir, number of snags per hectare with cavities, snag height, and percentage of open ground were higher in areas of saw-whet use than nonuse, whereas percentage of area dominated by white fir was higher in areas of nonuse (Table 2). Forward stepwise logistic regression resulted in a final model with 2 variables:
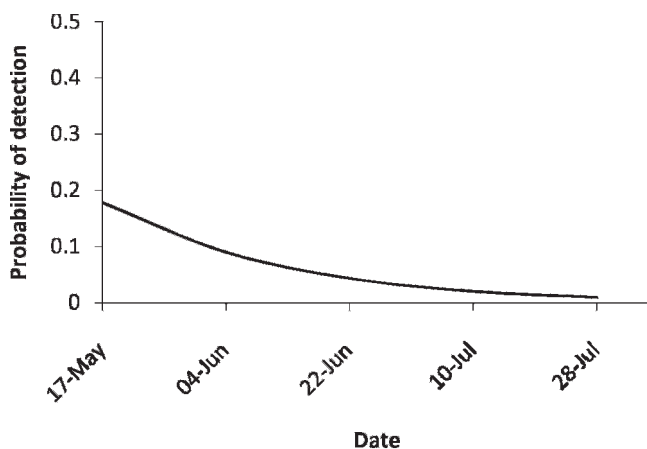

Figure 2. Predicted biweekly (2.5-week period) detection probabilities for northern saw-whet owls surveyed in the Lake Tahoe Basin, California, USA, May–July 2006. Probabilities generated from top-ranked model for 2006.
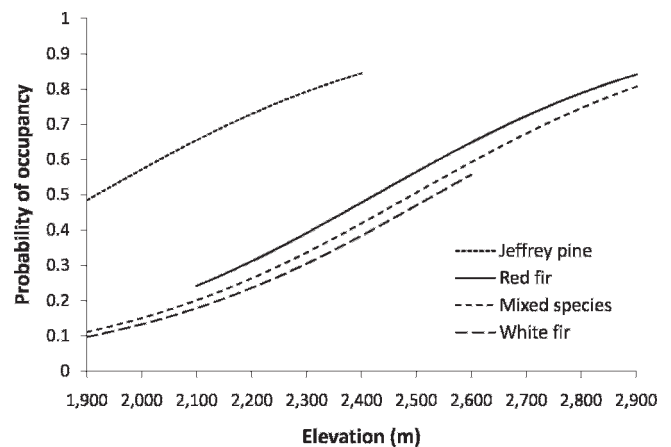

Figure 3. Predicted occupancy probabilities, incorporating site covariates of elevation and dominant tree species, for northern saw-whet owls surveyed in the Lake Tahoe Basin, California and Nevada, USA, March–June 2007. We clipped probability curves in the figure based on realistic maximum and minimum elevation of each tree species occurrence.

Table 2. Habitat characteristics of macrohabitat sites (average 260 ha) and microhabitat sites (20 ha) used by northern saw-whet owls and sites where we did not detect saw-whet owls (i.e., nonuse sites) during nocturnal broadcast surveys in the Lake Tahoe Basin, California and Nevada, USA, 2006–2007. We included habitat characteristics with $P \leq 0.15$ in forward stepwise logistic regression to develop a multivariate model estimating probability of saw-whet owl occupancy of a site.

Scale	Variable	Owl use sites			Owl nonuse sites			Mann–Whitney test	
		n	$\bar{x}$	SD	n	$\bar{x}$	SD	U	P
Macrohabitat	% canopy cover								
	Closed canopy (>60%)	25	7.5	14.9	9	13.8	21.3	96	0.514
	Open canopy (25–60%)	25	69.9	20.0	9	61.4	19.7	79	0.202
	Shrubland (10–25%)	25	17.1	12.6	9	17.7	12.3	107	0.848
	Herbaceous (1–10%)	25	3.6	6.9	9	6.3	7.8	80	0.216
	% cover by tree species								
	Jeffrey pine	25	16.8	28.4	9	4.3	12.8	80	0.216
	Red fir	25	26.5	26.4	9	8.4	21.8	56	0.030
	White fir	25	17.3	33.4	9	54.4	42.4	61	0.041
Microhabitat	Elevation (m)	52	2292	253	40	2192	262	776	0.037
	Distance to (m)								
	Forest opening	52	93	111	40	91	144	909	0.296
	Stream	52	438	451	40	542	558	953	0.493
	% canopy cover								
	Closed canopy (>60%)	52	10.7	21.4	40	9.7	21.9	943	0.373
	Open canopy (25–60%)	52	70.7	27.4	40	61.7	29.2	846	0.126
	Shrubland (10–25%)	52	15.3	14.9	40	22.1	24.5	973	0.597
	Herbaceous (1–10%)	52	3.1	7.3	40	5.8	12.1	952	0.386
	% cover by tree species								
	Jeffrey pine	52	17.7	33.3	40	10.07	24.5	959	0.394
	Lodgepole pine	52	8.0	17.5	40	3.9	13.5	895	0.132
	Red fir	52	24.9	30.4	40	11.7	25.6	793	0.032
	Subalpine conifer	52	6.7	11.9	40	5.0	13.8	892	0.151
	White fir	52	15.6	32.4	40	38.2	42.0	729	0.004
	Snag characteristics								
	No. snags/ha	40	41.1	25.2	40	46.0	35.9	776	0.814
	No. snags/ha ≥30 cm dbh	40	24.5	14.7	40	25.0	17.0	795	0.958
	No. snags/ha ≥40 cm dbh	40	16.2	10.1	40	16.6	11.8	797	0.973
	No. snags/ha with cavities	40	3.1	3.4	40	2.5	3.0	646	0.133
	Total no. cavities/ha	40	5.0	5.9	40	3.6	4.2	654	0.157
	No. snags/ha > decay class 1	40	24.4	19.3	40	23.5	22.6	744	0.587
	Snag dbh (cm)	40	42.2	12.2	40	38.9	8.5	685	0.266
	Snag ht (m)	40	10.5	2.3	40	9.6	2.2	599	0.053
	% open ground	40	61.0	17.7	40	53.4	19.7	623	0.089

percentage of area dominated by white fir and percentage of area classified as open canopy (Table 3; Fig. 4b). When we held open canopy at a fixed value, for a 1% increase in white fir cover odds of the site being occupied by a saw-whet decreased 1.7%; when holding white fir cover constant, there was a 1.5% increase in odds of saw-whet occupancy with a 1% increase in percentage of area classified as open canopy. The model fit the data to an acceptable degree with a Hosmer–Lemeshow value of 0.059 and correctly predicted

saw-whet use at 67.5% of sites with sensitivity and specificity of 70% and 65%, respectively (Table 3).

Although similar between use and nonuse sites, mean snag density differed in areas of the LTB relative to the dominant tree species. Snag density was approximately 68% higher (t_{78} = 3.48, P = 0.001) in sites dominated by white fir (primarily the west side of the basin; $\bar{x}$ = 58.9 snags/ha, SE = 5.98, n = 28) than in sites dominated by either red fir or Jeffrey pine ($\bar{x}$ = 35.3 snags/ha, SE = 3.80, n = 52).

Table 3. Logistic regression models we used to predict probability of northern saw-whet owl use and nonuse at macrohabitat sites (approx. 260 ha) and microhabitat sites (20 ha) in the Lake Tahoe Basin, California and Nevada, USA, 2006–2007.

Variable	Coeff.	SE	P	Exp(B)	Hosmer–Lemeshow goodness-of-fit P	Classification[a]		
						Sensitivity	Specificity	Overall
Macrohabitat								
Intercept	1.864	0.608	0.002	6.449				
White fir cover (%)	−0.024	0.011	0.021	0.976	0.304	88.0	44.4	76.5
Microhabitat								
Intercept	−0.571	0.612	0.351	0.565				
White fir cover (%)	−0.017	0.006	0.008	0.983				
Open canopy (%)	0.015	0.009	0.075	1.015	0.059	70.0	65.0	67.5

[a] % of correct classifications by the model; sensitivity is ability of the model to predict the event (i.e., owl use) and specificity is ability of the model to predict the nonevent (i.e., owl nonuse).
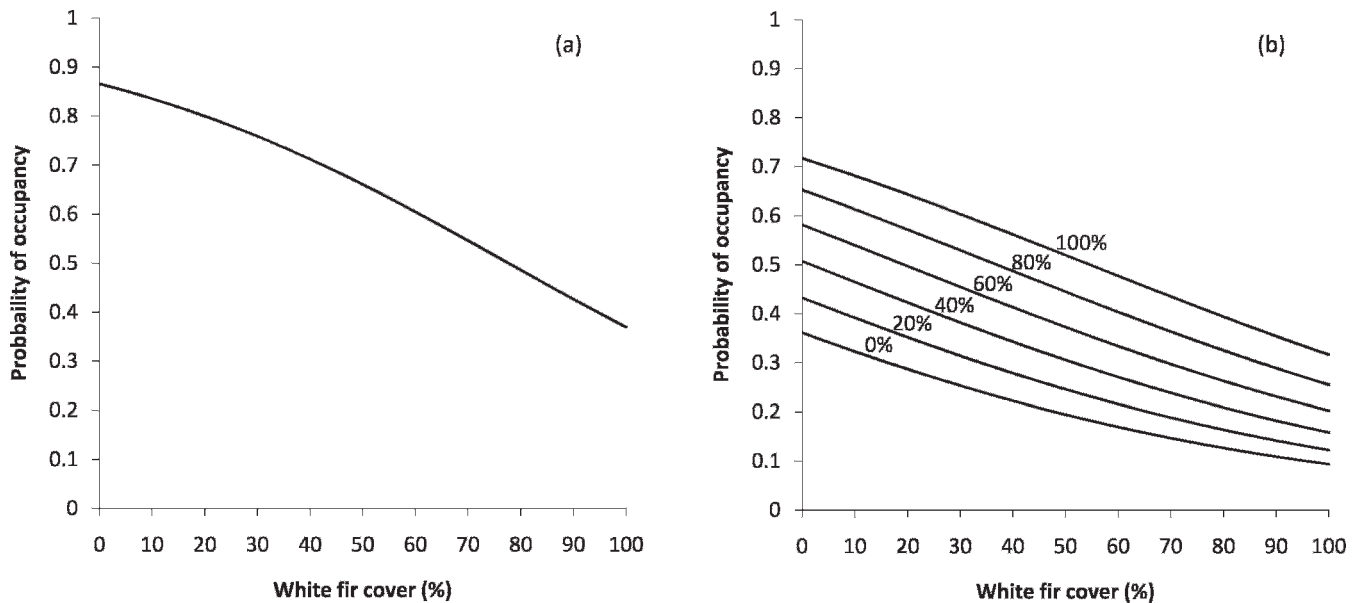
Figure 4. Predicted probabilities of northern saw-whet owl occupancy in the Lake Tahoe Basin, California and Nevada, USA, 2006–2007, in relation to percentage of area dominated by white fir at (a) macrohabitat sites and (b) microhabitat sites using the final models from forward stepwise logistic regression analyses. Influences of percentage area classified as open canopy is included for microhabitat sites (values listed above each curve).

DISCUSSION

Surveys beginning in March appeared to be more effective at detecting saw-whet owls than surveys initiated in May. Increased detection with early surveys was predictable given the owl's breeding behavior. Courtship and establishment of territories can begin as early as February and owls respond more readily to calls of conspecifics during this time (Palmer 1987, Cannings 1993). Although detectability of saw-whets was low (i.e., <0.30 either yr), we surveyed sites often enough (i.e., 3 or 6 times) to achieve low probabilities of false absences and, thus, unbiased estimates of occupancy. Detection probability may be higher still if surveys are started earlier in the season (i.e., Jan or Feb). If some owls were already paired and nesting, and thus less vocal when we initiated surveys in March, then our inferences of habitat associations would be applicable only to the responsive subset of the population that remained unpaired or nested later in the season. Earlier season surveys or intensive owl tracking and nest searching may resolve these unknowns.

Estimates of survey site occupancy indicated a positive relationship between elevation, dominant tree species, and saw-whet occupancy. Occupancy rates increased with elevation and in areas dominated by Jeffrey pine or red fir, whereas white fir was associated with the lowest rates of owl occupancy at any given elevation. Associations with Jeffrey pine, however, must be interpreted with caution, because only 9 of 128 survey sites were dominated by Jeffrey pine. Additionally, our assumption of spatial independence between survey points may have been violated in some areas where we suspected we detected the same owl at adjacent survey points. Lack of independence among sites can result in occupancy estimates with overestimated precision (MacKenzie et al. 2006). Although we could not distinguish between individual saw-whets, we tried to counteract possible

lack of independence by excluding from the analysis several owl detections that occurred at adjacent points.

Occupancy rates provide an estimate of the proportion of points occupied given the detection probability of the owl and, along with detection probability, can be used to determine adequate survey effort in future surveys (MacKenzie and Royle 2005). A balance can be achieved between feasible survey effort and a reasonable probability of not detecting an individual owl when it is present (i.e., a false absence), thus allowing for the development of reliable inferences regarding habitat associations. Based on a detection probability of 0.28 and occupancy rates of 0.10–0.80, 5–8 visits per survey site would achieve a low probability (0.05–0.15) of a false absence (MacKenzie and Royle 2005). Areas where the species is relatively uncommon would require fewer visits based on the suggestion that efficiency is increased when more sites are surveyed less often for rare species (MacKenzie and Royle 2005). Thus, survey protocols that span the central Sierra Nevada may vary based on the underlying habitat characteristics (e.g., elevation, dominant tree species). Given an average occupancy probability of 0.5, a detection probability of 0.28, and 6 visits throughout the survey season as noted above, approximately 40 sites would be required to achieve a standard error of 0.1 in occupancy estimates (MacKenzie and Royle 2005).

Stepwise logistic regression models showed significant, albeit weak, negative relationships between white fir and saw-whet owl occurrence. Sites dominated by white fir were correlated with a decrease in saw-whet occupancy at both the macrohabitat and microhabitat scales. The relationship was slightly stronger at the macrohabitat scale, indicating white fir may be of greater significance when determining saw-whet distribution at larger spatial scales (i.e., >250 ha). Although white fir exists in higher proportions today than

200 years ago (Manley et al. 2000), there is no indication in the literature as to why white fir would influence saw-whet occurrence. It is possible white fir was merely correlated with other factors that we did not measure. For example, differences in the biotic and abiotic conditions between white and red fir stands (e.g., Parker 1984, 1986) could affect abundance or availability of small mammals, the main prey of saw-whet owls (Cannings 1993, Coppeto et al. 2006).

The positive relationship between saw-whet occurrence and sites with a high percentage of open canopy maintained findings of previous researchers (e.g., Cannings 1987, Palmer 1987). Open canopy was influential at the microhabitat scale, indicating saw-whets may select areas dominated by open canopy at a scale more relevant to the size of their territory rather than at a larger landscape scale. Stands with open canopy may facilitate foraging by saw-whets and the ability for saw-whet vocalizations to be heard at greater distances (Cannings 1993).

Snag characteristics did not appear to influence distribution of saw-whets in the LTB. We estimated an average of 16 snags/ha for snags ≥40 cm diameter at breast height in the LTB, which exceeds USFS snag retention guidelines of 1–10 snags/ha (USFS 2004, Hutto 2006); therefore, potential nest sites for owls seem ample. Higher snag densities in the white fir–dominated western section of the LTB could be partly a result of increased mortality of white fir in the early 1990s due to epidemic levels of bark beetles (i.e., the fir engraver beetle [*Scolytus ventralis*]; Rizzo and Maloney 2000). Although snag densities were higher in white fir–dominated areas, where we detected fewer saw-whets, correlating snag densities with owl occurrence may be misguided. There are numerous differences between the western section of the basin and other areas of the basin besides the preponderance of snags and white fir that may be influencing absence of saw-whets; for example, the micro-climate is wetter, snow remains on the ground later into the year, and vehicle access is easier and more frequent.

Our work illustrates likely relationships in the Sierra Nevada between elevation, tree species, canopy cover, and saw-whet's use of an area. We suggest future research of habitat associations use stratified sampling relative to dominant tree species and elevation, to more rigorously test relationships with saw-whet occupancy, and initiate surveys in February to test whether detection increases or decreases relative to survey initiation in March. Furthermore, various sizes of survey sites could be tested to determine the appropriate size sampling unit for estimating saw-whet occupancy and detection.

MANAGEMENT IMPLICATIONS

Numerous projects are currently underway in the Sierra Nevada to decrease snag densities and return tree species composition to a state more similar to that of pre-European settlement (e.g., LTBMU 2008). Although our results indicate a decrease in snag densities or relative abundance of white fir may have a neutral or positive effect on saw-whet occurrence, monitoring the species over time would be necessary to determine the long-term effects of restoration. Nocturnal surveys for saw-whets in Sierra Nevada should begin no later than March. We recommend establishing sites that approximate the average territory size of saw-whets and establishing multiple survey points within those sites; detection at any one or several points during a visit would be considered one detection for the site. Our data suggest approximately 6 visits throughout the survey season at ≥40 sites would achieve a low standard error and increased reliability of trends in occupancy. Monitoring will indicate whether changes that occur with the saw-whet distribution in the LTB are due to management activities and whether those changes are proceeding in the desired direction. The desired direction for the LTB generally calls for maintaining biological integrity of the system (Manley et al. 2000), which includes maintaining historic levels of saw-whet owls rather than actively encouraging an increase in the species distribution.

ACKNOWLEDGMENTS

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