



Research Article

Diversity of Great Gray Owl Nest Sites and Nesting Habitats in California

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ABSTRACT The great gray owl (*Strix nebulosa*) is listed by the state of California as endangered, with a population estimate of fewer than 300 individuals in the state. Nest-site availability has been suggested as a limiting factor for population growth in California, but information on nest types and nesting habitat has been based on a small number of nests that may not fully represent the variety of conditions used by the species. We collated all known nesting records in the Sierra Nevada mountains of California since 1973 ($n = 56$) and then visited 47 of the nest sites to characterize habitat and compare them with paired reference sites. Great gray owls used a diversity of trees (8 species) and nest types. Although great gray owls in California are considered conifer-forest specialists, 30% of nests were in oak trees and 21% were below 1,000 m, which loosely corresponds to the lower conifer-zone limit. Across all elevations and tree species, degree of deterioration was the most important factor differentiating nest trees from paired reference trees at the same meadow, with nest trees being significantly more decayed. Nest trees (mean dbh = $100.5 \pm \text{SD } 30.3$ cm) were also significantly larger than reference trees. Canopy cover within 50 m of nest trees ($\bar{x} = 85.1 \pm 16.4\%$) was significantly greater at nest sites than at reference sites. At higher elevations, most nests were within 250 m of a meadow edge, but at lower elevations, 31% of nests were >750 m from the closest meadow. Based on these findings, we suggest that managers trying to promote great gray owl nesting maintain 4 or more large (100-cm dbh) snags per hectare in dense forests, especially near meadows. We also recommend increasing great gray owl survey effort in habitats and areas that may have been inadequately surveyed in the past. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS California, forest management, great gray owl, nest tree characteristics, nesting habitat, *Strix nebulosa*.

The great gray owl (*Strix nebulosa*) is the largest and arguably rarest owl in North America. An estimated 200–300 individuals live in California (Department of Fish and Game 2007), most of which belong to the central California endemic subspecies, *Strix nebulosa yosemitensis* (Hull et al. 2010, 2014) and nest within or near Yosemite National Park. The great gray owl is designated as endangered by the state of California and was recently classified as 1 of the 17 bird

species most vulnerable to anthropogenic climate change in the Sierra Nevada (Siegel et al. 2014). Suitable nesting opportunities and prey availability may be important factors limiting the population size of great gray owls in California (Winter 1985, 1986; Reid 1989; van Riper et al. 2013).

Great gray owls in California are known to nest in broken-top conifer snags near montane meadows (Winter 1986, Greene 1995, Sears 2002, van Riper and van Wagtenonk 2006, Keane et al. 2011), and to prefer a dense forest overstory (Greene 1995, Whitfield and Gaffney 1997, Keane et al. 2011). Other nesting habitat preferences may include north-facing slopes (Greene 1995), relatively flat terrain (Greene 1995, Keane et al. 2011), and forests with a high

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density of snags (Sears 2002). However, because of the species' rarity in California, and the difficulty in finding its nests, information on nest types and nesting habitat to date has been based on a small number of nests that may not fully represent habitat conditions that the species uses. There has never been a comprehensive effort to survey and describe systematically great gray owl nesting habitat across the species' range and diversity of habitats in California.

In recent years, anecdotal reports have mounted of great gray owls breeding in portions of the Sierra Nevada relatively distant from Yosemite, and nesting in oak trees. It has been unclear whether these more diverse nesting locales and habitats are anomalies, or instead indicate that the species may regularly nest in a broader diversity of environmental conditions in California than was previously known. Our purpose was to characterize the full range of nest trees and habitats known to be used by the species in California and draw preliminary inferences about their relative frequency. Obtaining a better understanding of nesting habitat selected by the species is critical for making more informed estimates of its population size in California, designing surveys to validate those estimates, and better defining habitat characteristics that land managers can promote to favor great gray owl nesting opportunities across the species' range in California.

STUDY AREA

This study took place on the western slope of the Sierra Nevada mountain range in California (Fig. 1) at various sites ranging in elevation from about 700 m to 2,400 m. The Sierra Nevada has a Mediterranean climate, with dry summers and most of the precipitation occurring between late fall and spring. We classified nest sites in Mariposa County and northward as northern, and sites in Madera County and southward as southern (Fig. 1; Beck and Winter 2000). At low-elevation sites (700–1,200 m in the north, 1,000–1,500 m in the south), the dominant tree species were ponderosa pine (*Pinus ponderosa*), black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*). At mid elevations (1,200–1,800 m in the north, 1,500–2,100 m in the south), the most common species were white fir (*Abies concolor*), incense-cedar, ponderosa pine, and red fir (*Abies magnifica*). At higher elevations (>1,800 m in the north and >2,100 m in the south), red fir, white fir, lodgepole pine (*Pinus contorta*), and Jeffrey pine (*Pinus jeffreyi*) dominated the overstory (elevation thresholds adopted from Beck and Winter 2000). Study sites were on lands managed by the United States Forest Service (USFS), Yosemite National Park, or private industry. Timber harvest and livestock grazing occur at varying intensities at and around the study sites on USFS and private lands but not in Yosemite National Park.

METHODS

Collating Nesting Records

We collated great gray owl nesting records from 1973 onward by searching statewide databases (Natural Resource

Information System, USFS 2013; California Natural Diversity Database, California Department of Fish and Wildlife 2014) and contacting all known researchers and land managers who have studied or monitored great gray owls in California. We ultimately located and included nest records from the California Department of Fish and Wildlife, the National Park Service, the USFS, Sierra Pacific Industries, and Southern California Edison. We limited our study to sites where an active nest had been visually confirmed (i.e., observations of fledglings without a nest were discarded) and where coordinates or other information permitted us to relocate the specific tree used for nesting. We excluded sites where owls nested in artificial nest structures because our aim was to characterize natural sites selected by owls.

Study Design

We visited nest sites and used a standardized protocol to describe nesting habitat at 3 spatial scales: 1) the nest tree, 2) the nest plot (a 50-m-radius plot centered on the nest), and 3) the nest stand (the forested portion of a 250-m-radius plot centered on the nest). We assessed nesting habitat at the scale of the plot because habitat structure proximal to the nest, although not necessarily representative of conditions across the larger stand (Gutiérrez et al. 1992), is likely to be important for factors such as thermal protection for eggs, nestlings, and incubating or brooding females, protection from aerial predators, and providing climbing perches for fledglings (Nero 1980, Bull and Henjum 1990). Our stand-level assessments were intended to describe forest structure components such as canopy cover and snag abundance at a broad spatial extent but still focusing on areas within the vicinity of the nest. We chose the plot- and stand-scales based on habitat selection of great gray owls and other *Strix* species at scales much larger than the nest tree (Nero 1980, Bull and Henjum 1990, Blakesley et al. 2005, Hamer et al. 2007).

In some cases, the nest trees we visited had not been used for nesting for many years, but we made every possible effort to ensure that we identified the correct tree. Some nest trees had been tagged by biologists upon original discovery, making confident relocation straightforward. When this was not the case, we consulted photographs and/or written descriptions if they were available, and when possible, we recruited local biologists familiar with the nest site to accompany us and ensure that we described the correct tree. However, there were instances when little information other than location coordinates was available. We therefore assigned 1 of 3 certainty categories (high, fair, and low) to each nest site, indicating our confidence that we had relocated the correct nest tree. When there were discrepancies in nest tree measurements between our data and data collected when the nest was originally discovered (5 instances), we used the original data.

We used a laser rangefinder to determine the distance from each nest tree to the edge of the nearest meadow or grassy opening where great gray owls could potentially forage. For each nest tree, we recorded the tree species, whether it was

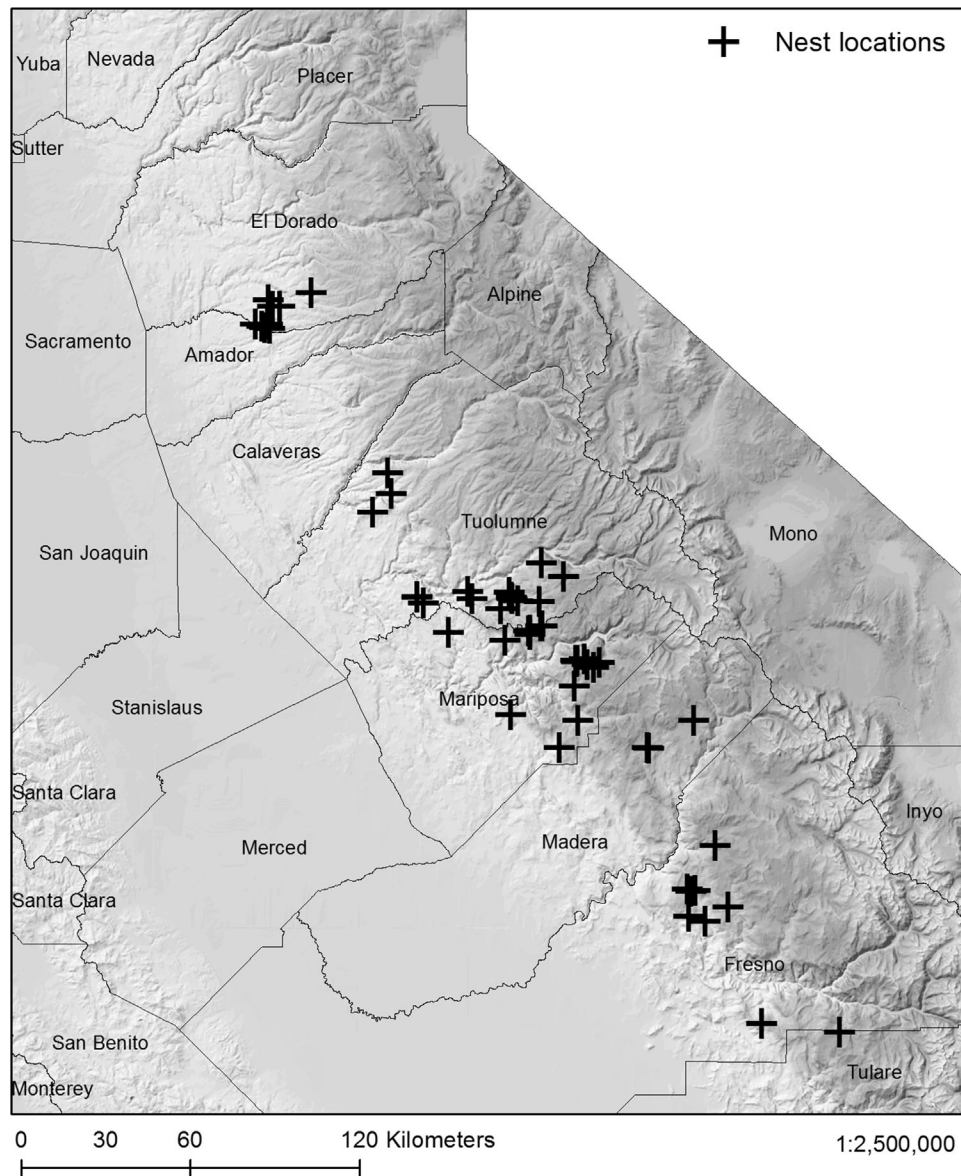


Figure 1. Locations of the 56 great gray owl nests identified in this study. The nests were discovered between 1973 and 2014 on lands managed by the United States Forest Service, Yosemite National Park, Sierra Pacific Industries, and Southern California Edison.

living or dead, its degree of deterioration, whether it was still standing or had fallen subsequent to being used for nesting, diameter at breast height (dbh), estimated diameter at the nest, and aspect of the slope at the base of the tree. We scored degree of deterioration visually from the ground on a categorical scale from 1 to 5, with 1 being an intact and non-deteriorating tree, 3 being a tree with up to 50% limb and bark loss and a broken top, and 5 being a tree with less than 20% of the bark remaining and a broken and rotten trunk. We measured tree and nest heights using a clinometer when the tree was still standing and a meter reel when it had fallen. We averaged canopy cover over nest trees from 4 measurements taken at the base of the tree with the observer facing each cardinal direction and using a convex spherical densiometer. We also recorded the slope aspect at the base of the tree and the trees position on the slope (e.g., crest, middle, toe, etc.).

In addition to describing the characteristics of each nest tree, we also wanted to compare the nest tree to the available trees near each nest site. For each nest site, we therefore collected all the same information (including tree characteristics as well as plot- and stand-level information) at and around a randomly selected reference tree. For each nest within 750 m of a meadow, we chose a paired reference tree in a geographic information system (GIS) by selecting a random location >100 m from the nest tree that was approximately the same distance from the edge of the nearest meadow as the nest tree. We considered nest trees >750 m from the nearest meadow not meadow-associated and in those cases, we selected a random forested location between 500 m and 2,000 m from the nest tree. We then selected a specific reference trees in the field by visiting the randomly selected location, and finding the closest living or dead standing tree greater than 60 cm dbh, or the next largest tree available if no trees >60 cm dbh occurred

within 50 m of the selected location (3 instances). We used a threshold of 60 cm dbh because 61 cm is the smallest great gray owl nest tree diameter previously described in California (Winter 1980).

At the 50-m-radius plots centered on the nest and reference trees, we visually determined the forest type (Mayer and Laudenslayer 1988) based on dominant tree species, counted snags >60 cm dbh, and estimated canopy cover by averaging 4 densiometer readings taken 25 m from the center of the plot in a random azimuth. We also used a slope-compensating angle gauge (Southwestern Environmental Consultants, Inc., Sedona, AZ) to estimate the basal area of trees in a variable-sized plot centered on the nest tree.

Within each 250-m-radius (approx. 20 ha) stand centered on the nest and reference trees, we randomly selected 4 non-overlapping 50-m-radius plots, where we collected the same data as at the plot level, but for these plots there was no bias introduced by a constraint that plots be centered on a large tree (Gutiérrez et al. 1992). We averaged data from these 4 plots to describe the overall stand.

Data Analysis

We analyzed nest tree and habitat data using R (version 3.1.0, cran.r-project.org, accessed 19 Jun 2013). When data were normally distributed according to a Shapiro test, we used a 2-tailed paired *t*-test to evaluate differences between nest and reference sites. Otherwise, we used a 2-sided paired Wilcoxon signed ranked test (the paired statistic is reported as *T*, the unpaired statistic is reported as *W*). We used analysis of variance (ANOVA) or Kruskal–Wallis (*F* and *H* statistic, respectively) tests to evaluate univariate differences among 3 or more categories, and a χ^2 test for categorical variables.

We assessed the importance of individual variables to nest tree selection in a multi-model framework using the information-theoretic approach (Burnham and Anderson 2002). We used the mixed-effects logistic regression model (GLMER) in the package LME4 (cran.r-project.org/package=lme4, accessed 14 Feb 2014) to determine criteria that differentiated nest trees from reference trees. We began by evaluating 10 a priori models that individually tested variables that have been previously described as important to nest-site selection of great gray owls. These variables were: elevation, species, firs, oaks, pines, degree of deterioration, dbh, canopy cover, aspect, and slope position. An 11th model was a null model, with no covariates. For all 11 models, we included site (i.e., each nest and reference tree pair) as a random effect. We reduced the analysis to only trees with complete data for the 10 variables, resulting in a sample size of 32. We compared all models using Akaike's Information Criterion corrected for finite sample size (AIC_c ; package AICCMODAVG, cran.r-project.org/package=AICcmoavg, accessed 14 Feb 2014). After comparing AIC_c support for the 10 variables relative to a null model, we additionally ran post hoc models that evaluated additive effects of 2 variables. We tested only for additive effects of variables that showed improvement upon (i.e., AIC_c scores less than) the null model.

We also compared nest-site characteristics among sites on lands managed by the USFS, Yosemite National Park, and private landholders to examine differences that may have resulted from differing management regimes. Throughout the text, values are presented as means $\pm$ standard deviation. The sample size of various nest-site metrics differs by characteristic measured (depending, for example, on whether the nest tree was located with confidence or whether we could determine where in the tree the nest had been situated) and is provided in the text.

RESULTS

Nest Trees

In total, 57 great gray owl nest sites across California met our criteria, but we excluded a site that was on private land near the Oregon border in Modoc County because of its spatial isolation and our inability to obtain access permission. We believe these 56 nests include every known nest tree in California discovered between 1973 and 2014. Six of the 56 nests were last known to be used between 1987 and 1995, 9 were last used between 2000 and 2005, 28 were last used between 2006 and 2010, and 12 were last used after 2011. Information about year of use was lacking for 1 nest. The 56 nest sites spanned 207 km from north to south, from El Dorado to Tulare County (Fig. 1), and varied in elevation from 691 m to 2,420 m (Fig. 2). Twenty-eight nests were on USFS lands, 18 were within Yosemite National Park, and 10 were on privately owned land.

We visited 41 of the 56 sites during August–October 2013, and 6 during July–August 2014. We were unable to visit 8 sites because of inaccessibility caused by the Rim Fire in late summer of 2013, and 1 site for which we obtained information during preparation of this manuscript. We located 35 nest trees with high or fair certainty. We obtained data that had been collected previously (including tree species, and in some cases tree height, dbh, and other information) for 8 of the 12 nests with low certainty and 8 of the 9 nests that we could not visit for logistical reasons; thus we had some information for 51 nest trees. Notably, nest tree conditions and nesting habitat characteristics may have changed somewhat between the last time a site was used for nesting and our habitat assessment in 2013 or 2014. We looked for evidence of such changes (e.g., signs of recent fire or logging) during field visits and also reviewed fire history data (based on fire boundaries delineated in the Vegetation Burn Severity—1984 to 2013 database; USFS 2014). Twelve sites exhibited evidence of selective logging or fire occurring post-nesting, but we nevertheless assessed nest tree and habitat characteristics that were present at the time of our visit because in all cases the disturbances appeared relatively minor and unlikely to have substantially altered the variables we were assessing.

Seventy-two percent of nests were within 250 m of a meadow, but 10 of the 47 nests we visited were farther than 750 m from the nearest meadow or grassy opening (Fig. 3). Of these 10, 6 were below the overall mean nest elevation of 1,527 m and 4 were above it. Of the 37 nests that were

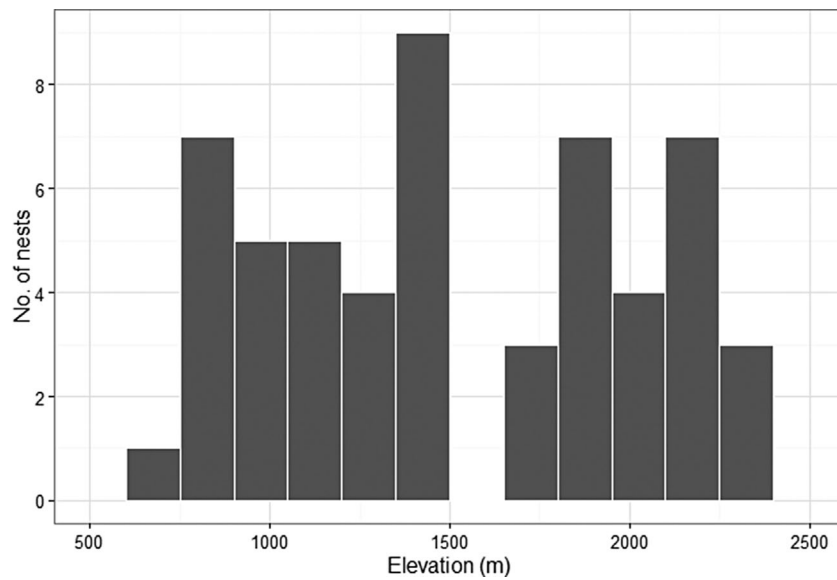


Figure 2. Elevational distribution of great gray owl nest sites in California discovered between 1973 and 2014 ($n = 56$). Nests ranged from 691 m to 2,420 m, with a mean elevation of $1,527 \pm 517$ m.

<750 m from a meadow, the mean distance to meadow edge was 101 ± 104 m. The most common tree species used for nesting was red fir ($n = 15$), followed by black oak ($n = 14$), white fir ($n = 11$), ponderosa pine ($n = 5$), lodgepole pine ($n = 2$), valley oak (*Quercus lobata*, $n = 2$), Douglas-fir ($n = 1$), and gray pine (*Pinus sabiniana*; $n = 1$; Fig. 4). Thirty-two of the 35 conifer nest trees were certainly or likely dead at the time of nesting, as were 6 of the 16 oaks (Fig. 4). A larger ($\chi^2_1 = 30.2$, $P \leq 0.001$) portion of nest trees (75%) than reference trees (16%) were dead. At lower elevations, great gray owls used black oaks and valley oaks disproportionately more and ponderosa pines and Douglas-firs disproportionately less for nesting than they were available at nest sites. None of the nests were in incense-cedar or sugar pine although these species were generally present or abundant at lower and mid-elevation sites. At higher elevation sites, owls nested in the 3 most common tree

species at the nest sites, red fir, white fir, and lodgepole pine, but did not use sugar pine or Jeffrey pine when they were present.

Nest trees ($n = 43$) had a mean dbh of 100.5 ± 30.3 cm, which was larger ($T = 456$, $P = 0.05$) than the mean dbh of reference trees (89.5 ± 27.9 cm). However, the reference tree was larger than its paired nest tree at 32% of 38 sites. The mean dbh of conifers ($\bar{x} = 99.5 \pm 29.7$ cm, $n = 28$) and hardwoods ($\bar{x} = 102.3 \pm 32.3$ cm, $n = 15$) used for nesting was nearly identical ($W = 210$, $P = 1$). There was no difference ($F_{2,40} = 1.696$, $P = 0.20$) in dbh of nest trees among Yosemite National Park ($\bar{x} = 111.1 \pm 29.8$ cm, $n = 15$), USFS ($\bar{x} = 92.2 \pm 31.9$ cm, $n = 19$), and privately owned sites ($\bar{x} = 100.3 \pm 24.8$ cm, $n = 9$). The mean estimated bole diameter at the nest was 68.2 ± 23.1 cm, and mean height of the nest was 14.3 ± 5.9 m (Table 1). Nest trees ($n = 44$, of which 32 had broken tops) were shorter ($t_{38} = 4.19$, $P \leq 0.001$) than reference trees (Table 1), although 23% of nest trees were taller than their paired reference tree. Nest trees were more deteriorated (mean degree of deterioration 3.1 ± 1.5 , $n = 35$; $T = 403$, $P \leq 0.001$) than reference trees ($\bar{x} = 1.5 \pm 1.0$), even after excluding 8 nest trees (and their paired reference trees) that had fallen and further deteriorated since the time of nesting ($T = 192.5$, $P \leq 0.001$). At 9% of 34 sites, reference trees had a higher deterioration rating than their paired nest trees. We found no significant difference ($T = 489$, $P = 0.43$) in canopy cover measured at nest and reference trees (Table 1). Seventeen nest trees were on west-facing slopes, 12 on north-facing, 10 on east-facing, and 7 on south-facing, which was not different from a proportional distribution ($\chi^2_3 = 4.6$, $P = 0.20$).

Of 42 sites at which we could determine the type of nest used, 27 were broken-top nests (e.g., nests in the depression created by the rotting bole where the top of the tree had broken off), 10 were in oak cavities formed either by broken tops or sloughed off limbs, 3 were in structures created by forking branches, 1 was a platform nest on top of a broad, flat

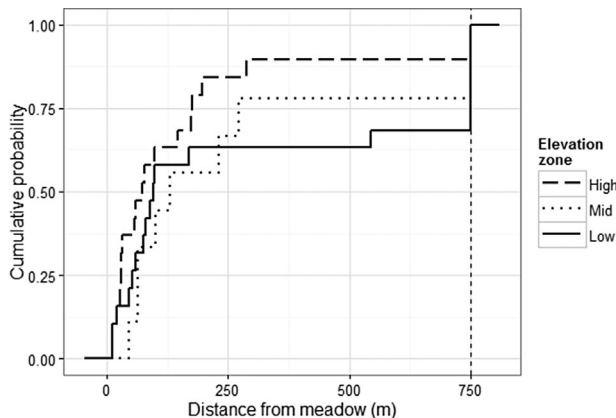


Figure 3. Cumulative distribution of the distance of great gray owl nests from the nearest meadow for nests in California discovered between 1973 and 2014. Distances >750 m are truncated. Thresholds for high, mid, and low elevations are latitude-dependent and detailed in the text.

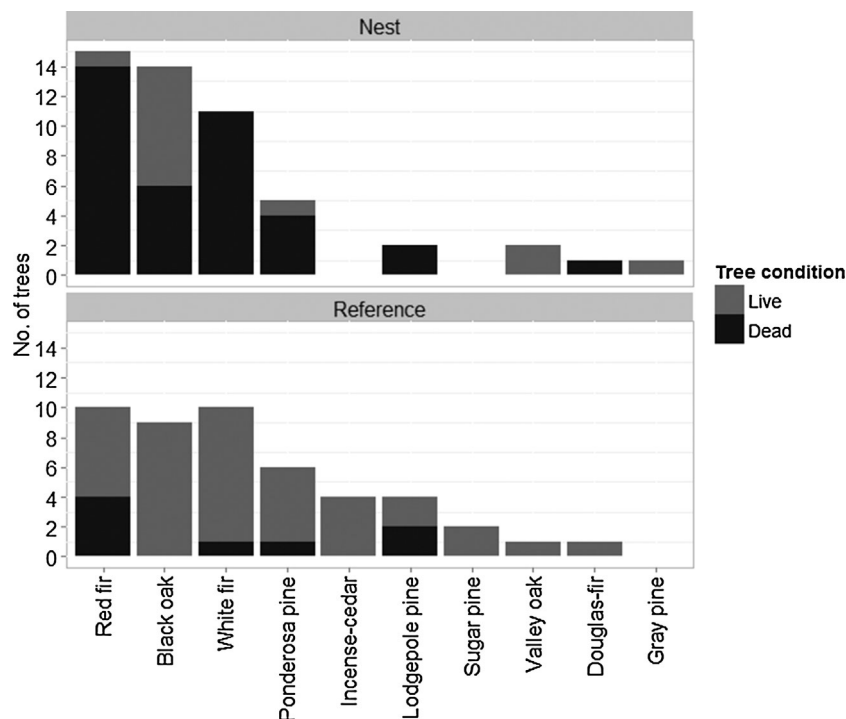


Figure 4. Species and condition (live or dead) of 51 trees used for nesting by great gray owls in California between 1973 and 2014, and 47 paired reference trees.

branch, and 1 was a stick nest built by another bird species (Figs. 5 and 6). All 22 fir nests were in broken tops, whereas nests in other tree species were in a greater diversity of structures (Fig. 5). The dbh of the tree with a stick nest was 44 cm, much smaller than all of the other nest trees.

We evaluated 10 univariate models plus a null model seeking to explain nest tree versus random tree selection. Of the tested models, 2 variables (degree of deterioration and dbh) were improvements upon the null model, with full model weight ($w=1.0$) given to degree of deterioration (Table 2). A single post-hoc model testing for additive effects of both degree of deterioration and dbh was weakly supported compared to a model with just degree of deterioration ($\Delta AIC_c = -0.74$).

Plot-Scale Analysis

At the scale of the 50-m-radius nest plot, great gray owls nested primarily in Sierran mixed conifer forest and red fir forest but also used white fir, lodgepole pine, and montane hardwood conifer forest types (Fig. 7). Although 16 of the nest trees were oaks, 15 of the oak nests were in forests that

nevertheless were dominated by conifers, and conifers were present but not clearly dominant at the remaining site (Fig. 7). Two nests were in plots that had been burned by stand-altering fire shortly (3 and 6 years) before the nest was used, and 1 nest was in a plot that burned while nesting was in progress. At least 2 additional nests were in plots where canopy cover was substantially reduced by timber harvest shortly (2 and 5 years) prior to nesting. Canopy cover was greater ($T=612.5$, $P=0.01$, $n=41$) at nest plots ($\bar{x}=85.1 \pm 16.4\%$) than at reference plots ($\bar{x}=74.9 \pm 22.5\%$), although reference plots had greater canopy cover than their paired nest plots at 32% of 41 sites. Density of large snags (>60 cm dbh) was higher ($T=358$, $P=0.03$) at nest than reference plots (Table 3). Density of large snags differed among Yosemite National Park, USFS, and private sites at nest ($H_2=24.1$, $P=0.001$) and reference plots ($H_2=16.1$, $P=0.001$; Table 3).

When pooled across land ownership classes or compared within each ownership class, there were no significant differences in conifer, hardwood, and snag basal area between nest and reference plots (Table 3). Snag basal area differed,

Table 1. Characteristics of great gray owl nest trees in California, 1973–2014, and paired reference trees.

	Nest trees			Reference trees		
	$\bar{x} \pm SD$	Range	<i>n</i>	$\bar{x} \pm SD$	Range	<i>n</i>
Dbh (cm)	100.5 $\pm$ 30.3	44–192	43	89.5 $\pm$ 27.9	41–185	47
Diameter at nest (cm)	68.2 $\pm$ 23.1	37–140	30			
Tree height (m)	18.7 $\pm$ 8.1	6.1–38.8	44	32.3 $\pm$ 13.4	4.0–59.3	47
Nest height (m)	14.3 $\pm$ 5.9	5.0–30.0	44			
Canopy cover (%)	81.5 $\pm$ 15.2	47.0–100	47	82.2 $\pm$ 15.9	25.6–99.2	47

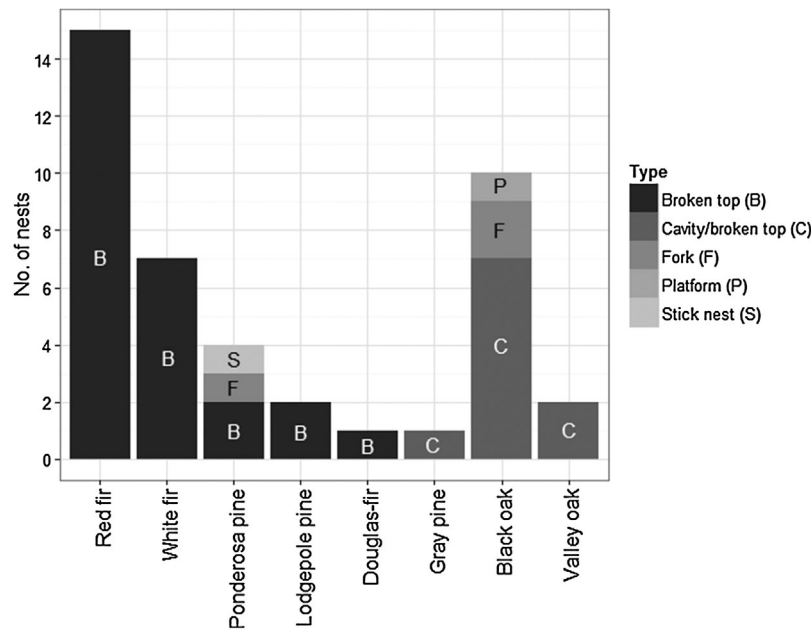


Figure 5. Nest types used by great gray owls in each species of tree for nests in California discovered between 1973 and 2014. Most nests in conifers were broken-top nests. One nest in a ponderosa pine was a stick nest constructed by another bird species, and another was in a fork created by branches that emerged around a broken top (candelabrum). The nest in the gray pine was in a cavity created by a sloughed-off branch. One black oak nest was on a large branch that provided a platform for the bird to nest on. Cavity and broken-top nests were grouped together for oaks because it was not always possible to tell whether a rotted hollow was due to a branch or the top of the main trunk breaking off.



Figure 6. Examples of the diversity of nests used by great gray owls in California from 1973 to 2014. In the top panel, from left to right, are nests in the broken top of a red fir snag, broken top of a ponderosa pine snag, broken top of a lodgepole pine snag, and a fork in the branches of a live ponderosa pine. In the bottom panel, from left to right, are nests in the broken top of a live black oak bole, an upright cavity left by a sloughed-off secondary trunk in a live gray pine, a fork in 2 large branches of a live black oak, and a platform nest on a flat section of a branch in a live black oak (indicated by the arrow).

Table 2. Results of 10 single-variable mixed-effects logistic regression models, a null model, and 1 post hoc additive model of nest tree selection by great gray owls in California between 1973 and 2014. We compared models using Akaike's Information Criterion corrected for finite sample size (AIC_c) and present number of parameters (K).

	K	AIC_c	ΔAIC_c	AIC_c weight
Degree deterioration + dbh	4	66.07	-0.74	
Degree deterioration	3	66.81	0.00	1.0
Dbh	3	92.27	25.46	0.0
Null (site as random effect)	2	92.92	26.11	0.0
Canopy cover	3	93.61	26.80	0.0
Aspect	3	93.73	26.91	0.0
Fir	3	94.56	27.75	0.0
Pine	3	94.65	27.83	0.0
Oak	3	94.81	28.00	0.0
Slope position	7	94.84	28.02	0.0
Elevation	3	95.12	28.31	0.0
Species	11	106.04	39.22	0.0

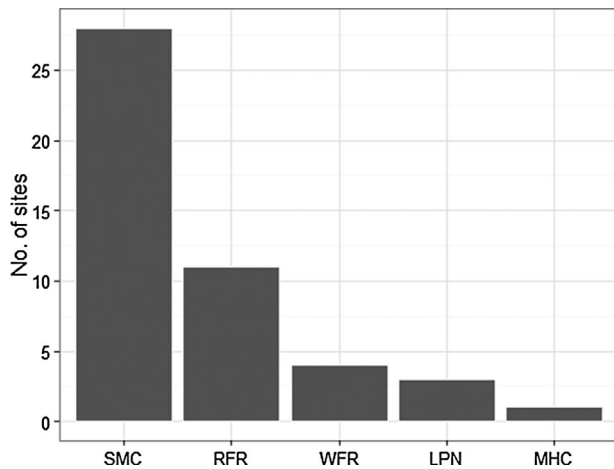


Figure 7. Dominant forest types (Mayer and Laudenslayer 1988) within a 50-m radius of the 47 great gray owl nests in California we visited included Sierran mixed conifer (SMC), red fir (RFR), white fir (WFR), lodgepole pine (LPN), and montane hardwood conifer (MHC). All nests were active between 1973 and 2014.

however, among the ownership classes. At nest plots, snag basal area was higher at Yosemite sites than USFS ($W=202$, $P=0.007$) and private sites ($W=85$, $P=0.02$), but there was no difference between USFS and private stands. At reference stands, snag basal area was also higher at Yosemite than USFS ($W=32.5$, $P=0.001$) and private sites ($W=14$, $P=0.005$) but was not different between USFS and private sites.

Stand-Scale Analysis

At the stand scale, 56% of the nest sites were in Sierran mixed conifer forest, 20% were in red fir, 12% were in white fir, and the rest of the sites were in ponderosa pine, lodgepole pine, or montane hardwood-conifer forests. Canopy cover at nest stands ($\bar{x}=80.3 \pm 14.3\%$) was not different ($T=304.5$, $P=0.10$) than at reference stands ($75.1 \pm 15.5\%$; $n=41$ for each). Density of large snags (>60 cm dbh) did not differ between nest and reference stands (Table 3). Large snag density differed among Yosemite National Park, USFS, and private sites at nest ($H_2=18.1$, $P=0.001$) and reference stands ($H_2=19.7$, $P=0.001$).

There were no significant differences in conifer, hardwood, and snag basal area between nest and reference stands when pooled across ownership classes or compared within each ownership class (Table 3). However, snag basal area differed among the ownership classes. At nest stands, snag basal area was higher at Yosemite sites than USFS ($W=61.5$, $P=0.005$) and private sites ($W=9$, $P=0.001$), but there was no difference between USFS and private stands. At reference stands, snag basal area was also higher at Yosemite than USFS ($W=230$, $P=0.001$) and private sites ($W=1$, $P=0.001$) but was not different between USFS and private sites.

DISCUSSION

Great gray owls nested in a greater diversity of locations across the species' range in California than previously documented, but several patterns in habitat usage are nevertheless evident and support some novel management and survey recommendations. Long considered a montane to upper-montane meadow specialist in California, 12 of the 56

Table 3. Estimated basal area (m^2/ha) and the density of snags >60 cm dbh (snags/ha) within 50 m (plot-scale) and 250 m (stand-scale) of great gray owl nest trees active between 1973 and 2014 and reference trees in Yosemite National Park (YNP), on United States Forest Service lands (USFS), and at privately owned sites. Values are presented as mean $\pm$ standard deviation.

	YNP ($n=13$)		USFS ($n=20$)		Private ($n=8$)		Pooled mean ($n=41$)	
	Nest	Reference	Nest	Reference	Nest	Reference	Nest	Reference
Plot-scale								
Basal area								
All live	72.0 $\pm$ 35.4	72.4 $\pm$ 29.5	61.8 $\pm$ 32.2	59.5 $\pm$ 36.7	55.7 $\pm$ 31.9	58.0 $\pm$ 75.5	62.3 $\pm$ 34.0	63.3 $\pm$ 44.0
Conifers	72.0 $\pm$ 35.4	72.4 $\pm$ 29.5	55.8 $\pm$ 35.7	55.1 $\pm$ 39.2	42.5 $\pm$ 36.0	49.9 $\pm$ 68.3	57.0 $\pm$ 37.0	59.6 $\pm$ 43.5
Hardwoods			6.0 $\pm$ 10.0	4.4 $\pm$ 5.9	13.2 $\pm$ 15.4	8.0 $\pm$ 10.3	5.4 $\pm$ 10.4	3.7 $\pm$ 6.6
All snags	22.6 $\pm$ 20.7	21.5 $\pm$ 14.2	8.5 $\pm$ 11.3	2.8 $\pm$ 4.3	5.2 $\pm$ 6.2	3.4 $\pm$ 4.8	12.0 $\pm$ 15.6	8.8 $\pm$ 12.3
Snag density	9.0 $\pm$ 5.1	6.6 $\pm$ 6.7	2.2 $\pm$ 3.4	1.1 $\pm$ 1.8	0.3 $\pm$ 0.6	0.3 $\pm$ 0.9	4.0 $\pm$ 5.1	2.7 $\pm$ 4.7
Stand-scale								
Basal area								
All live	80.6 $\pm$ 28.7	71.8 $\pm$ 23.2	60.9 $\pm$ 22.0	54.6 $\pm$ 24.8	44.4 $\pm$ 17.4	35.2 $\pm$ 14.9	64.0 $\pm$ 26.4	56.3 $\pm$ 25.7
Conifers	80.3 $\pm$ 28.9	71.0 $\pm$ 24.1	54.3 $\pm$ 26.4	49.9 $\pm$ 26.4	32.2 $\pm$ 21.3	24.5 $\pm$ 18.8	58.2 $\pm$ 31.0	51.7 $\pm$ 29.0
Hardwoods	0.3 $\pm$ 0.7	0.8 $\pm$ 3.0	6.7 $\pm$ 9.0	4.7 $\pm$ 5.5	12.2 $\pm$ 10.1	10.6 $\pm$ 18.8	5.7 $\pm$ 8.7	4.6 $\pm$ 7.4
All snags	18.4 $\pm$ 13.3	16.8 $\pm$ 10.6	4.5 $\pm$ 4.1	4.6 $\pm$ 4.8	2.1 $\pm$ 1.6	1.4 $\pm$ 1.4	8.4 $\pm$ 10.5	7.9 $\pm$ 9.2
Snag density	5.2 $\pm$ 3.9	5.2 $\pm$ 3.0	1.5 $\pm$ 1.6	1.2 $\pm$ 1.2	0.4 $\pm$ 0.2	0.2 $\pm$ 0.4	2.5 $\pm$ 3.1	2.3 $\pm$ 2.8

great gray owl nest-site records (21%) we collated were of nests below 1,000 m in elevation. Thirty percent of nest trees were oaks, primarily within Sierran mixed conifer forest. Although the relative importance to great gray owls of the lowest portion of the montane zone in the Sierra Nevada needs further assessment, particularly in relation to nest success, it seems clear that nesting in lower-elevation conifer-dominated forest just above the transition from oak woodlands is not anomalous. Likewise, although it has been thought that the great gray owls in California (Winter 1986) and elsewhere (Bouchart 1991) nest rather exclusively near the edges of montane meadows, 20% of the nest sites we assessed were only weakly, if at all, associated with montane meadows. On the aggregate, nests were indeed quite proximal to meadows, but 10 of 47 nest sites were more than 750 m from the nearest meadow or grassy opening and 6 of these were at lower elevations.

Availability of large snags is likely a particularly important factor affecting nesting habitat suitability. Even though our study design constrained most reference trees to have dbh >60 cm, nest trees were larger still, averaging 100 cm in dbh. Great gray owls chose trees with markedly similar diameters whether they were oaks or conifers and regardless of land ownership and the relative availability of large (>60 cm) snags and trees. In our regression analysis, tree dbh did not appear to be very important for discriminating nest trees from reference trees, but this could be because of the size constraints of reference trees. More generally, our regression analysis compared habitat used for nesting with available habitat that was nearby; it may be that forest characteristics at reference stands adjacent to the same meadows as nest stands differ far less from nest stands than do forest characteristics adjacent to unoccupied meadows, which we did not assess. Nest trees were, on average, 13.6 m shorter than reference trees, but we believe this is because of the strong negative correlation between tree height and degree of deterioration rather than a preference for short trees.

Although great gray owls in California demonstrate flexibility in the type of nest used, the great majority of nests were in broken tops of boles or in cavities formed by broken off trunks or large limbs, structures that require some degree of at least localized tree deterioration. Suitable nest trees may only stand for a few years (Bull 1983, Landram et al. 2002) once they reach the necessary level of decay to provide a nesting site. One study in the Sierra Nevada found that snags in advanced stages of decay usually fell within 5 years (Morrison and Raphael 1993); at least 29% of nests trees we visited had fallen since the time of nesting. Even where great gray owls are already nesting successfully, managers should consider the standing crop of appropriate nest trees, and whether recruitment in the coming decades is likely to counterbalance attrition. Managing for clusters of large trees, especially firs, and a mosaic of many age classes may therefore be vital to retaining suitable nesting sites over time. At lower and middle elevations, managing for oak retention and recruitment may be more beneficial than managing for large conifers because numbers of oaks have

been substantially reduced by historical timber and rangeland practices (Standiford et al. 1996), and oaks are relatively more resilient to fire (Collins et al. 2011) and continue standing and even growing after considerable deterioration occurs. Great gray owls nested in a greater variety of tree species than previously documented, but, consistent with findings in Greene (1995), they never used incense-cedar, sugar pine, or Jeffrey pine for nesting, even when those species were common in the nest stand. Incense-cedar and pines do not deteriorate as readily as firs (Lowell and Cahill 1996). Even after they die, the wood often stays robust until it splinters, rather than forming heart rot that can be conducive to a broken-top nest. Incense-cedars have, however, been used successfully to create long-lasting artificial nests that have been accepted by great gray owls (Winter 1982).

Dense canopy cover around the nest is likely important to great gray owls. Canopy cover directly above nest trees did not differ from reference trees likely because many more reference trees than nest trees were alive, and the cover from live foliage of the focal tree itself increased densiometer readings at the reference trees. Another possibility is that when snags are limited, great gray owls may select nesting trees based only on size and deterioration, regardless of canopy cover. At the plot scale (50-m-radius around nest), canopy cover around great gray owl nests was indeed greater than cover at reference plots. However, at the stand scale (250-m-radius around the nest), we found no evidence that great gray owls select for denser cover, suggesting that either cover is only important in the immediate vicinity of the nest, where it provides protection against predators (Whitfield and Gaffney 1997), thermal regulation (Beck and Smith 1987) and branching opportunities that aid young birds that are still unable to fly competently to begin to venture out of the nest (Nero 1980, Bull and Henjum 1990), or that stand-level canopy cover varies relatively little within forested areas where great gray owls nest.

Finally, our findings point to several research needs, such as linking reproductive success to habitat conditions and increasing survey effort. Although we now have more information on characteristics of nest trees, nest success and productivity data are needed to fully understand optimal habitat conditions that support and promote great gray owl reproduction. Substantially increasing survey effort throughout previously under-surveyed portions of great gray owl's breeding range in California is also needed to better understand the distribution and abundance of the species throughout the state. In particular, Sierran mixed conifer forest near the lower boundary of the montane zone, especially where large-diameter black oaks are common, should be prioritized for surveys and conservation-oriented management. Although higher emphasis can be placed on forest stands near meadows with potential foraging habitat, otherwise appropriate stands that are not proximal to meadows merit survey effort as well, not just in and around Yosemite, but at least as far north as Plumas County and as far south as Fresno County. In particular, there is a gap in nest records from Calaveras and Amador Counties, and

between El Dorado and Plumas Counties, where great gray owl fledglings have been observed but nests have never been located (A. Shufelberger, Sierra Pacific Industries, and C. Stermer, California Department of Fish and Wildlife, personal observation).

MANAGEMENT IMPLICATIONS

Perhaps the most important thing land managers can do to facilitate great gray owl nesting is to recruit and retain suitable nest trees across a variety of forest types between 700 m and 2,400 m on the western slope of the Sierra Nevada. Where promoting great gray owl nesting is a management goal, our data suggest maintaining a minimum of 4 large snags per hectare that are at or above the mean nest tree size (100 cm dbh), although owls may less frequently use snags as small as 60 cm dbh. Where possible, dense canopy cover (85% or greater) should be maintained in stands with suitably high snag density. Particularly at middle and higher elevations, management should focus on the suggested snag and canopy density within 250 m of meadows, which provide suitable foraging habitat. In lower elevation Sierran mixed conifer forests, where our results indicate great gray owls nest more frequently in oaks and nests are often not proximal to meadows, recruitment and retention of large oaks irrespective of proximity to meadows may be most beneficial to the owls. In great gray owl range where timber harvest or other management practices reduce the recruitment of large snags, managers should actively recruit snags and protect large deteriorating snags from removal. Recognizing that suitable nest trees are ephemeral resources, managers should strive to maintain an appropriate balance of live trees and deteriorating snags. Finally, we urge biologists across great gray owl range in California to increase survey effort in previously under-surveyed areas and habitats where the species may nest, particularly near the lower boundary of the montane zone.

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