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GREAT GRAY OWLS NESTING IN ATYPICAL, LOW-ELEVATION HABITAT IN THE SIERRA NEVADA, CALIFORNIA

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Abstract.—Great Gray Owls (*Strix nebulosa*) in the Sierra Nevada were once believed to nest strictly within mid-elevation conifer forests in close proximity to montane meadows. However, recent observations of Great Gray Owls nesting at lower elevations suggest the lower-montane zone of the Sierra Nevada, where oak-dominated woodlands transition to conifer-dominated forests, may also provide habitat for this California-listed endangered species. We describe the reproductive success, apparent occupancy rate, and habitat associated with eight Great Gray Owl nests monitored between 2006–2014 on commercial timberlands in the lower-montane zone of the central Sierra Nevada, California. Reproductive success was high, with several breeding attempts producing three fledglings, and an average of 1.9 ± 0.9 young fledged during 21 breeding attempts. Apparent occupancy rates were also high (87.5% ± 20.9%) in the years following the discovery of a territory. Nests were in large-diameter ($\bar{x} = 102.5$ cm) trees, but smaller-diameter (25.4–50.7 cm) trees dominated the surrounding landscape, which was composed primarily of dense mixed conifer and hardwood forest interspersed with annual grasslands. Our results suggest that the lower-montane zone of the Sierra Nevada, though at the geographic limit of Great Gray Owl's elevational range, can provide suitable nesting habitat. We used Maxent to identify potential Great Gray Owl nesting habitat throughout the lower-montane zone of the Sierra Nevada based on conditions around the nests we studied. Our model identified areas within 10 counties of the central and northern Sierra Nevada that we recommend be surveyed for Great Gray Owls. Identifying such locations could focus survey efforts to determine if this cryptic species is nesting in the identified areas, perhaps in numbers that may be a significant component of the very small statewide population.

Key Words: *Great Gray Owl*; Strix nebulosa; *atypical nesting habitat*; *lower-montane zone*; *reproductive rate*; *Sierra Nevada.*

INDIVIDUOS DE *STRIX NEBULOSA* ANIDANDO EN UN HÁBITAT ATÍPICO DE BAJA ALTITUD EN SIERRA NEVADA, CALIFORNIA

Resumen.—En el pasado se creía que en Sierra Nevada los individuos de *Strix nebulosa* anidaban estrictamente dentro de los bosques de coníferas de mediana altitud cercanos a las praderas montanas. Sin embargo, observaciones recientes de individuos de *S. nebulosa* anidando a altitudes menores sugieren que la zona montana baja de Sierra Nevada, en la zona de transición entre los bosques dominados por robles y los bosques dominados por coníferas, también puede proveer hábitat para esta especie presente en la lista de especies en peligro de California. Describimos el éxito reproductor, la tasa aparente de ocupación y el hábitat asociado con ocho nidos de *S. nebulosa* seguidos entre 2006–2014 presentes en bosques maderables comerciales en la zona montana baja del centro de Sierra Nevada, California. El éxito reproductor fue alto, con numerosos intentos reproductivos que produjeron tres volantones y un promedio de 1.9 ± 0.9 pollos que dejaron el nido en 21 intentos reproductivos. Las tasas aparentes de ocupación también fueron altas (87.5% ± 20.9%) en los años que siguieron al descubrimiento de un territorio. Los nidos se ubicaron en árboles de gran diámetro ($\bar{x} = 102.5$ cm), pero los árboles de menor diámetro (25.4–50.7 cm) dominaron el paisaje circundante, el cual estuvo compuesto principalmente por un bosque denso mixto

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de coníferas y árboles de madera noble entremezclados con pastizales anuales. Nuestros resultados sugieren que la zona montana baja de Sierra Nevada, aunque está ubicada en el límite geográfico del rango altitudinal de *S. nebulosa*, puede proporcionar hábitat apropiado para la cría. Utilizamos Maxent para identificar el hábitat de cría potencial a lo largo de la zona montana baja de Sierra Nevada en base a las condiciones registradas alrededor de los nidos que estudiamos. Nuestro modelo identificó áreas dentro de 10 condados del centro y norte de Sierra Nevada que recomendamos sean censados en busca de *S. nebulosa.* La identificación de este tipo de lugares puede concentrar los esfuerzos de los censos para determinar si esta especie críptica se encuentra anidando en las áreas identificadas, quizás en números que pueden ser un componente importante de la muy pequeña población estatal.

[Traducción del equipo editorial]

The Great Gray Owl (*Strix nebulosa*) is classified as an endangered species in California (Winter 1980, CNDDB 2015), where the Sierra Nevada mountains constitute the southernmost extent of its range in North America, and the statewide population is estimated to be around 100–200 individuals (Greene 1995, Hull et al. 2010). Initial research in California classified the Great Gray Owl as strictly a montane conifer specialist that breeds above 1200 m in the Sierra Nevada, largely in association with meadows (Winter 1986). More recent observations led to the inclusion of the lower-montane zone, down to 700 m, as part of Great Gray Owl breeding range (Bull and Duncan 1993, Beck and Winter 2000, van Riper and van Wagtendonk 2006, Hull et al. 2014). However, the lower extent of the species' elevation range has generally not been considered an important component of its nesting habitat in California. Mid-elevation coniferous forests in Yosemite National Park and Stanislaus and Sierra National forests have been viewed as the core of the owl's range in the state (Hull et al. 2010, van Riper et al. 2013).

A recent compilation of all known nesting records in California (including the nests described here) suggested that the lower-montane zone, defined here as the transition zone between oak-dominated woodlands and conifer-dominated forests, may be more important for California's Great Gray Owl population than previously thought, as 21% of 56 documented nest sites were below 1000 m (Wu et al. 2015). However, it remains unclear whether nests in the lower-montane zone produce fledglings at similar rates as nests in more typical habitat for Great Gray Owls in California (i.e., mid-elevation forests adjacent to montane meadows), or instead if the zone might function as a sink for the species. In some cases, habitat at the limits of a species' range is marginal (Holt 2003) and is associated with reduced fitness (Arnaud-Haond et al. 2006, Angert and Schemske 2007), particularly when climate-imposed range limits are related to the species' physiological limits (Gaston 2003, Bateman et al. 2015). Yet this is not true universally and some studies have found little evidence of reduced habitat quality or fitness near the limit of a species' range (Griffith and Watson 2006, Samis and Eckert 2009, Sexton et al. 2009).

In 2006, one of us (KR) discovered three Great Gray Owl fledglings on lower-montane, commercial timberlands owned and managed by Sierra Pacific Industries (SPI) in El Dorado County, California. The presence of nesting Great Gray Owls was unexpected because the area, at 700–1000 m above sea level, was lower than any previously described nest in the Sierra Nevada, was miles from the nearest cluster of known breeding sites, and was devoid of any montane meadows. During subsequent years, SPI personnel initiated and expanded surveys for Great Gray Owl occupancy and reproduction throughout the vicinity where the fledglings were discovered.

Here we evaluate multiyear data from Great Gray Owl nests in the lower-montane zone of the central Sierra Nevada to assess reproductive success and estimate annual occupancy rates, and compare them with similar data from mid-elevation nests elsewhere in the region. Although our sample size is small, Great Gray Owl nests are rarely found in California (only 56 nests found since 1973; Wu et al. 2015) and little is known of their reproductive output. We also describe habitat characteristics around the nests and use the information to develop a predictive landscape-level model for identifying areas with similar characteristics across the lower-montane zone of the Sierra Nevada. Although the winter distribution of Great Gray Owls in California has been previously modeled (Jepsen et al. 2011), a predictive model for breeding habitat is lacking. Our goal was not to model all potential breeding habitat for Great Gray Owls in the Sierra Nevada, but rather, to focus on determining locations within the lower-montane zone that may be suitable nesting habitat for the species based on characteristics of known nesting locations within our limited study area. Identifying such locations could focus survey efforts to determine if

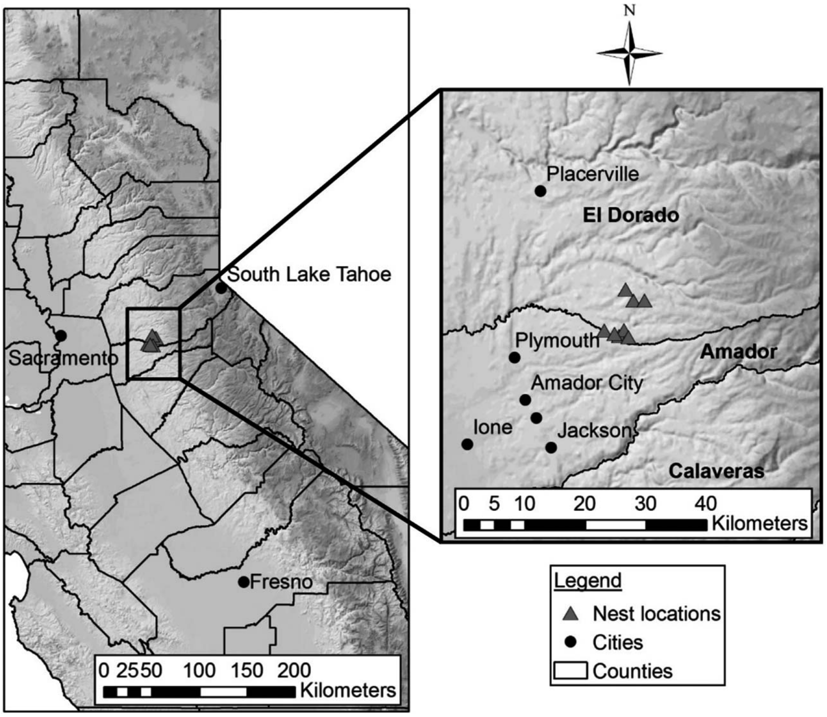

Figure 1. Great Gray Owl nest locations in the lower-montane zone (nests range from 691–1023 masl) of the Sierra Nevada, California.

this cryptic species is nesting in the identified areas, perhaps in numbers that may be a significant component of the small statewide population.

METHODS

Occupancy and Reproductive Surveys. Since the discovery of a breeding territory and three fledglings in 2006, SPI has been conducting Great Gray Owl surveys on its property near Plymouth, CA, in El Dorado County (Fig. 1), targeting areas with habitat similar to where the first territory was found. Survey stations were established approximately 160 to 480 m apart across 4123 ha identified as possible Great Gray Owl habitat within an overall study area of 6242 ha, and were surveyed at least three times per year, with some areas receiving up to six surveys in some years. Following Beck and Winter (2000), a Great Gray Owl survey protocol developed specifically for the Sierra Nevada and widely used in California, the first survey was conducted during the courtship period (15 February–20 March), the second survey during incubation (20 March–20 April), and the third survey during the post-fledgling period (20 May–15 June), when young are most vocal. Each survey consisted of a 6-min period of vocalization playbacks (Beck and Winter 2000). Where surveys confirmed pair status but did not reveal nest locations, observers returned once or twice in June to search for young. When nests were found, they were monitored to determine nest success and the number of young that fledged. To avoid disturbing nesting owls, and because nests were frequently in rotting portions of trees that would be dangerous to climb, surveyors did not climb to assess clutch sizes. We determined the number of distinct territories based on the number of simultaneously occupied sites (with occupancy defined as the daytime detection of one or more owls) and by banding and resighting owls when possible. We used observed detections and non-detections to calculate apparent occupancy rates. A formal occupancy framework model (MacKenzie et al. 2003) could not be implemented due to small sample size.

Local Habitat Assessment. We assessed habitat around Great Gray Owl nests (Fig. 1), within circular plots of three different radii: 270, 450, and 900 m. The radii of these plots were based on previous studies of Great Gray Owl home-range sizes for males

(270 m; van Riper and van Wagtendonk 2006), females (450 m; van Riper and van Wagtendonk 2006) and pairs (900 m; Winter 1986). Using remotely sensed data, we assessed the percent cover (Evans et al. 2014) of the following habitat characteristics within each radius around each nest: vegetation type (e.g., conifer, hardwood, herbaceous, shrub), California Wildlife Habitat Relationship (CWHR) habitat type, canopy closure class, and dominant overstory tree size class (CALVEG 2009) in ArcMap 10.3 (ESRI 2014). We tested for differences in the distribution of habitat characteristics present within the three different plot sizes using one-way ANOVA tests in R.

To assess the accuracy and applicability of remotely sensed data for describing local conditions within our study area, we ground-truthed remotely sensed data with vegetation cover data collected by SPI personnel for stand inventory purposes using variable-radius plots placed every 264 m along lines 200 m apart. However, several nests were located close to SPI property boundaries, and because the extent of available plot data was limited to SPI-owned land, the amount of remotely sensed data that we ground-truthed was constrained when a portion of a specific radius around a nest was outside SPI property boundaries. For radii around Great Gray Owl nest locations with field data for the entire radius (n = 6 at 270-m-radius, n = 4 at 450-m-radius, and none at 900-m-radius), we used Pearson's correlation to assess similarity between field-collected habitat variables and corresponding remotely sensed habitat variables to confirm that remotely sensed data accurately described actual landscape conditions.

Potential Nesting Habitat Elsewhere in the Lower-montane Zone. We used the algorithm Maxent (Phillips et al. 2006, 2010) to identify locations throughout the lower-montane zone of the Sierra Nevada that have habitat characteristics similar to those of the Great Gray Owl nest areas. Maxent models species distribution by finding the maximum entropy in species' occurrence locations in relation to a set of environmental variables (Phillips et al. 2006). In Maxent, areas that are not presences (i.e., not nest locations) are used to represent background information rather than being interpreted as absences (Phillips et al. 2006, Franklin and Miller 2009). We used Maxent because it has been shown to outperform other modeling methods with small sample sizes (Pearson et al. 2007, Wisz et al. 2008), performs well with presence-only data (Elith et al. 2006) and incorporates ensemble methods that can increase the robustness of the final prediction (Araújo and New 2007). We built a model based on Great Gray Owl nest locations and 19 environmental variables (Table 1) assessed at a 30-m pixel resolution. We used all nest locations in our study area to train the model and selected 5001 iterations for the model run (Phillips and Dudik 2008, Franklin and Miller 2009). We graphed response curves to determine how each variable affected the model and used area under the receiver operating characteristic (ROC; Swets 1988) curve (AUC) as a threshold for model validation (Manel et al. 2001). We extrapolated our model to the portion of the western slope of the Sierra Nevada that makes up ±1 SD (585–1129 m) of the elevation range of the Great Gray Owl nests in our study area, correcting for latitude based on a 1-km change in latitude corresponding to a 1-m change in elevation (Hopkins 1938). When extrapolating our model, we used a similarity index ranging from 0–1 where a value of 1 represents areas predicted to be most similar to the habitat at our nest locations.

RESULTS

Apparent Occupancy and Reproductive Success. We monitored 21 breeding attempts (where eggs were laid; Steenhof 1987), representing eight distinct nests on six territories, from 2006–2014 (Table 2). Nests were first found during the incubation, nestling, or fledging stages; all such breeding attempts were included in our calculations of reproductive rate, regardless of when they were discovered. The number of young produced during these breeding attempts ranged from 0–3 (Table 3), and averaged 1.9 ± 0.9 (Table 4). At 19 successful breeding attempts (where at least one young fledged; Steenhof 1987), reproduction averaged 2.1 ± 0.9 young per successful nest. The average number of young produced appeared to be higher than corresponding rates observed at mid-elevation nests in Yosemite National Park (Table 3, Table 4; Keane et al. 2011 and Yosemite National Park unpubl. data), and was comparable to rates documented elsewhere in the species' range (Table 4). The six territories discovered in our study area were largely occupied continually following initial detection (87.5% ± 20.9% apparent occupancy during all subsequent years after initial discovery; Table 2). One of the eight nests was reused subsequent to its first discovery.

Local Habitat Assessment. Field-collected nest stand data, including tree density and basal area of

Table 1. Environmental variables derived for landscape model analyses. All variables except slope were assessed as percent cover within three radii (270 m, 450 m, and 900 m) around known nests. California Wildlife Habitat Relationships (CWHR) habitat types, canopy closure classes, and tree diameter classes are from CALVEG (2009) and described in Mayer and Laudenslayer (1988).

VARIABLE CATEGORY	ABBREVIATION	VARIABLE DESCRIPTION
CWHR habitat type[a]	AGS	Annual grassland
	BOP	Blue oak-foothill pine
	BOW	Blue oak woodland
	DFR	Douglas-fir
	MCH	Mixed chaparral
	MHC	Montane hardwood-conifer
	MHW	Montane hardwood
	PPN	Ponderosa pine
	SMC	Sierran mixed conifer
	VOW	Valley oak woodland
Canopy closure class[a]	Dense	≥60% canopy closure
	Moderate	40–59.9% canopy closure
	Open	25–39.9% canopy closure
	Sparse	10–24.9% canopy closure
Overstory tree diameter class[a]	Pole dbh	12.7–25.3 cm dbh
	Small dbh	25.4–50.7 cm dbh
	Medium dbh	50.8–76.1 cm dbh
	Large dbh	≥76.2 cm dbh
Topography[b]	Slope	Average percent slope

[a] U.S.D.A. Forest Service Pacific Southwest Region–CALVEG.
[b] U.S. Geological Survey National Elevation Data (30-m resolution).

conifers, hardwoods, and all trees combined, were highly correlated with similar values derived from remote-sensed data ($R > 0.80$ for each forest structure and composition variable we assessed). The distributions of cover types and classes did not differ significantly ($P > 0.05$) among the three radii (270-m, 450-m, and 900-m) for any of the 18 habitat variables assessed. For simplicity, we therefore report landscape-level habitat values for the 900-m-radius scale only, as that represents an area large enough to potentially encompass a home range of a nesting Great Gray Owl pair (Winter 1986, van Riper and van Wagtendonk 2006).

Nest sites ranged from 691–1023 m above sea level in mixed conifer-oak forests dominated by ponderosa pine (*Pinus ponderosa*), black oak (*Quercus kelloggii*), Douglas-fir (*Pseudotsuga menziesii*), interior live oak (*Quercus wislizeni*), and incense-cedar (*Calocedrus decurrens*) and interspersed with grasslands. Nest trees had an average diameter at breast height (dbh) of 102.5 ± 23.9 cm and nests were 10.3 ± 2.4 m aboveground. Trees used for nesting included living black

Table 2. Occupancy patterns over 9 yr at six Great Gray Owl territories containing eight nests. '1' and '0' stand for occupied (by breeding or nonbreeding owls) and unoccupied, respectively, and '-' means not surveyed that year. Apparent occupancy rate following the initial year of detection was 87.5% ± 20.9%.

	YEAR								
TERRITORY	2006	2007	2008	2009	2010	2011	2012	2013	2014
A[a]	1	1	1	1	1	1	1	0	0
B	-	-	1	1	1	1	1	1	1
C	-	-	1	1	1	1	1	1	1
D	-	-	1	1	1	1	0	0	0
E	-	-	-	-	-	-	1	1	1
F	-	-	-	-	-	-	1	1	1

[a] Territory A contained nests 1, 2, and 3, as numbered in Fig. 2, which were used by the same banded male in different years. Territories B–F correspond sequentially to nests 4–8 in Fig. 2.

Table 3. Number of observed breeding attempts producing zero, one, two, or three young at lower-montane nests on SPI land between 2006 and 2014 (this study), and in Yosemite National Park between 2004 and 2014 (Keane et al. 2011 and Yosemite National Park unpubl. data). "Young" includes both nestlings and fledglings. Many of the counts of young in Yosemite were not based on intensive nest monitoring efforts, but rather resulted from opportunistic discoveries of fledglings during occupancy surveys, possibly biasing the results. Breeding attempts producing zero young in both studies may also be underestimated, as failed nests were less likely to be discovered, particularly later in the nesting season.

	FREQUENCY OF OBSERVED BREEDING ATTEMPTS PRODUCING *n* YOUNG				
LOCATION	0	1	2	3	OBSERVED BREEDING ATTEMPTS
Lower-montane	2 (10%)	4 (19%)	9 (43%)	6 (29%)	21
Yosemite National Park	3 (7%)	21 (49%)	19 (44%)	0	43

oak (*n* = 3), dead black oak (*n* = 2), dead Douglas-fir (*n* = 1), living gray pine (*Pinus sabiniana*, *n* = 1), and living valley oak (*Quercus lobata*, *n* = 1). Five nests were in broken tops or cavities formed where branches broke off black and valley oaks, two in broken tops of a gray pine and a Douglas-fir, and one on a natural platform on a large branch of a black oak. The average slope within 900 m of nests was 11.7% ± 2.2%. The aspect of the nest sites were north (*n* = 4), north-northeast (*n* = 1), and southwest (*n* = 3). Distance from nests to meadows (Sierra Nevada multi-source meadows polygon; Fryjoff-Hung and Viers 2012) averaged 9.8 ± 1.3 km. The average distance to grassy forest openings that could potentially be used for foraging was 75 m and ranged from 20–170 m. The most common silviculture practice around nests from 1998 to 2007 was "shelterwood removal cuts" (35.4 ± 32.8% of the 900-m radius area), in which young trees were not cut but older, mature trees were harvested. Additional silvicultural practices in the vicinity were often used to create even-aged stands and included "alternative prescriptions" (7.5 ± 11.2%, usually resembling regeneration harvests with patches of trees), "selection cuts" (5.5 ± 4.0%, in which individual or small groups of trees from all size classes were removed, leaving a significant portion of the stand after harvest), "regeneration harvests" (2.8 ± 5.7%, also known as clearcuts, in which all trees outside of riparian areas were removed and the area was replanted), "sanitation salvage" (2.3 ± 6.4%, in which insect-infested or diseased trees were removed), "rehabilitation" (1.5 ± 3.1%, in which vegetation and trees were removed and the area was replanted), "fuel breaks" (0.5 ± 1.0 %, in which trees and vegetation were removed to create a fuel break to reduce the potential for wildfire), and "seed tree removal cuts" (0.3 ± 0.8 %, in which no more than 15 predominant trees per acre were removed and small regenerating trees were retained). The remainder of the area around nests had no record of recent harvest activity.

Landscapes within a 900-m-radius of the eight nests were composed of 60.9 ± 24.6% coniferous forest, 26.9 ± 1.9% hardwood forest, 10.7 ± 8.6% herbaceous cover, and 1.6 ± 1.6% shrub cover (Fig. 2A). Within those cover types, 10 CWHR habitat types were present. On average, the sites were made up of 23.4 ± 11.9%

Table 4. Great Gray Owl reproductive output from lower-montane breeding attempts (this study) compared to results from Yosemite National Park, northeastern Oregon, and Idaho and Wyoming. "Young" includes both nestlings and fledglings. Across studies, observed breeding attempts may not be fully representative of all breeding attempts, as nests were discovered throughout the breeding season and failed nests were less likely to be discovered than successful ones.

		YOUNG PER OBSERVED BREEDING ATTEMPT		YOUNG PER SUCCESSFUL BREEDING ATTEMPT
LOCATION	OBSERVED BREEDING ATTEMPTS	RANGE	(MEAN ± SD)	(MEAN ± SD)
Lower-montane	21	0–3	1.9 ± 0.9	2.1 ± 0.9
Yosemite National Park[a]	43	0–2	1.4 ± 0.6	1.5 ± 0.5
Northeastern Oregon[b]	62	0–5	1.7 ± 1.2	2.2 ± 0.9
Idaho and Wyoming[c]	15	0–4	2.6 ± 1.4	3.0 ± 0.9

[a] Keane et al. (2011) and Yosemite National Park (unpubl. data).

[b] Bull and Henjum (1990).

[c] Franklin (1988).

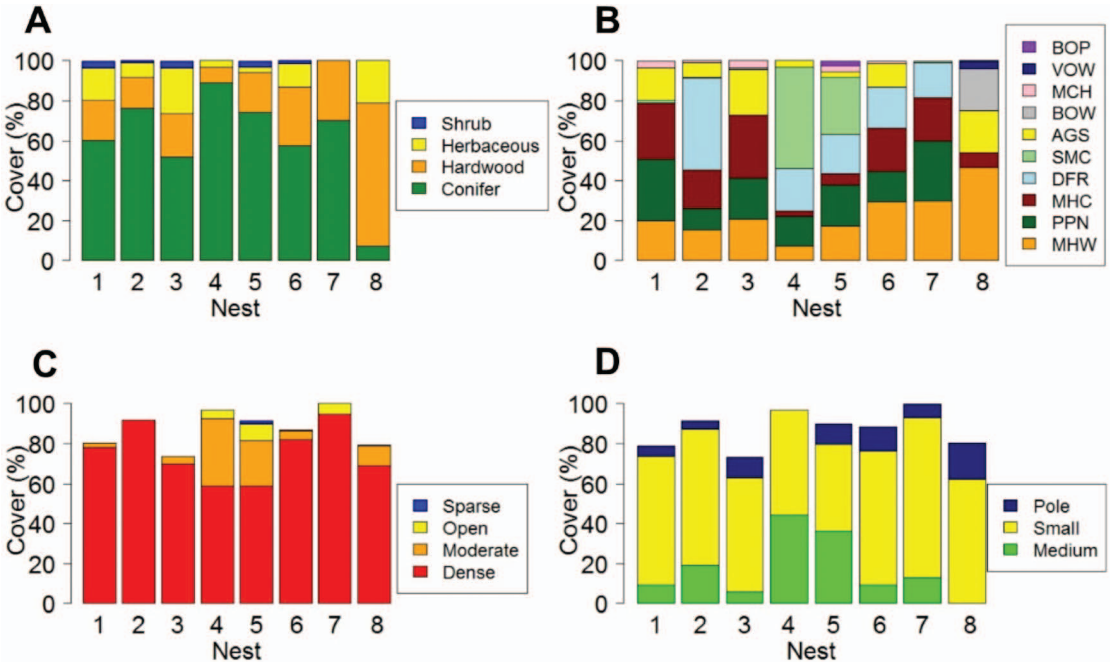

Figure 2. Percent cover of various habitat characteristics within a 900-m circular radius of Great Gray Owl nests in the lower-montane zone, including: (A) vegetation type, (B) California Wildlife Habitat Relationship (CWHR) habitat type (BOP = blue oak-foothill pine, VOW = valley oak woodland, MCH = mixed chaparral, BOW = blue oak woodland, AGS = annual grassland, SMC = Sierran mixed conifer, DFR = Douglas-fir, MHC = montane hardwood-conifer, PPN = ponderosa pine, MHW = montane hardwood), (C) canopy closure, and (D) overstory tree diameter class (all abbreviations defined in Table 1; Mayer and Laudenslayer 1988).

montane hardwood (MHW), 17.8 ± 10.1% ponderosa pine (PPN), 17.3 ± 10.7% montane hardwood-conifer (MHC), 15.6 ± 15.7% Douglas-fir (DFR), and 10.7 ± 8.6% annual grassland (AGS), and several other classes at low percent coverages (Fig. 2B). Canopy closure within 900 m of the nests averaged 75.4 ± 13.7% dense (≥60%) canopy, followed by 9.6 ± 12.3% moderate (40–59.9%) canopy, 2.3 ± 3.1% open (25–39.9%) canopy, and 0.2 ± 0.6% sparse (10–24.9%) canopy; Fig. 2C). Overstory tree diameter classes around nests averaged 61.8 ± 11.1% small-dbh trees (25.4–50.7 cm), followed by 17.2 ± 15.5% medium-dbh trees (50.8–76.1 cm), and 8.4 ± 5.5% very-small-dbh trees ("pole" sized; 12.7–25.3 cm; Fig. 2D).

Potential Nesting Habitat Elsewhere in the Lower-montane Zone. Our Maxent-generated similarity index assessed the similarity of potential habitat throughout the lower-montane zone of the Sierra Nevada to the nest sites we studied. The index incorporated seven variables, with Dense, Smalldbh, Largedbh, and slope contributing most heavily (Fig. 3). However, Dense, Smalldbh, and Poledbh were the variables that influenced the model fit the most, based on how much each influenced AUC if it was the only variable in the model (Table 5). The model AUC was 0.963 and the conditions for locations with a similarity index of >0.60 for lower-montane Great Gray Owl nesting habitat included >70% dense cover, >50% cover by small-dbh trees, and <1% cover by large-dbh trees (Table 5). When we extrapolated from the model across the lower montane zone of the Sierra Nevada, the areas predicted to have the highest similarity index to lower-montane Great Gray Owl nesting habitat were clustered in lower-elevation portions of Calaveras, Amador, El Dorado, Placer, Nevada, Yuba, Sierra, Butte, Plumas, and Tehama counties (Fig. 4).

DISCUSSION

Occupancy and Reproductive Success. Our study area in the lower-montane zone of the Sierra Nevada does not appear to be a population sink for Great

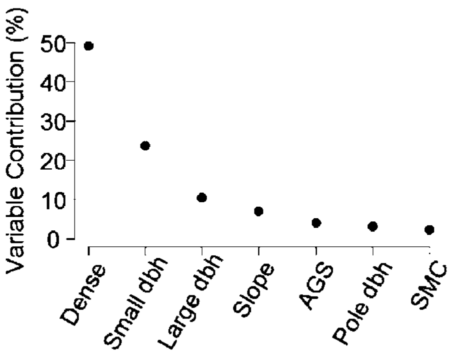

Figure 3. Contribution of the most important variables to the landscape-level model of Great Gray Owl lower-montane nesting habitat (AGS = annual grassland, SMC = Sierran mixed conifer).

Gray Owls; in fact, the number of young produced per successful breeding attempt appeared to be slightly greater than at Yosemite National Park, which is generally considered the core of Great Gray Owl's range in California (van Riper and van Wagtendonk 2006, Hull et al. 2014). However, one important caveat is that because we continued to find nests throughout the reproductive cycle and add them to our study, our calculated rates of young per breeding attempt may be biased upward, because nests that failed early in the season were less likely to be detected and included than those that were successful. Another caveat is that whereas we generally undertook nest-search efforts following pair detection, most counts of young in Yosemite were based on opportunistic discoveries (S. Stock pers. comm.), which means that reproductive rates may not be entirely comparable. We nonetheless compared our results to the minimum reproductive output recorded at nests in Yosemite National Park due to the lack of other reproductive data in California, though the differences in methodology precluded more rigorous statistical testing. Nests producing three young have previously been noted only twice in California: once in 1999 near Shaver Lake, Fresno County (U.S. Forest Service 2013), and another in 2007 also near Shaver Lake (C. Stermer pers. comm.), but the output of the latter might have been attributable to supplemental feeding. Yet six of 21 (29%) breeding attempts we observed at our lower-montane study site produced three young, indicating an apparent sufficiency of resources for nesting owls.

Table 5. The approximate values for >60% similarity with Great Gray Owl nesting territories in our lower-montane study area based on Maxent response curves. Variables are listed in order of model gain alone, which indicates the importance of each variable for fitting the model if Maxent were to use only that variable in the model; for comparison the model gain when all listed variables are included in the model is 1.58.

VARIABLE	APPROXIMATE VALUES FOR >60% SIMILARITY	MODEL GAIN ALONE
Dense	>70% Dense cover	0.74
Smalldbh	>50% Small dbh tree cover	0.60
Poledbh	<16% Pole dbh tree cover	0.29
Largedbh	<1% Large dbh tree cover	0.09
Slope	<15% Slope	0.08
AGS	0–100% AGS cover	0.01
SMC	<40% SMC cover	0

Similarly, the apparent occupancy rate at our study site was high: once a territory was discovered, it had an 87.5% chance of being occupied in any future year that it was monitored. Our small sample size precluded formal occupancy analysis and estimation of detection probability, but any false absences due to imperfect detection would mean that the true occupancy rate was even higher. Taken together, high productivity and high apparent occupancy rates at our study site suggest that, in this instance, habitat is not marginal even though our study area is likely near the geographic edge of the owls' range (Kawecki 2008, Samis and Eckert 2009, Sexton et al. 2009). Our data cannot explain why the number of young produced per successful nesting at our study area appeared to be higher than at Yosemite National Park (but note the caveats above), but possible factors worthy of further study include a shorter and milder winter associated with the lower elevation, and perhaps the presence of different prey species or more abundant prey.

Local Habitat Assessment. Great Gray Owls in our lower-montane area most frequently (six of eight nests) utilized large oaks for nesting, but relative proportions of hardwood and conifer cover were highly variable within a 900-m radius of the nests. Half of the nesting territories had 70–89% conifer cover and 8–30% hardwood cover, whereas the remaining sites had 8–60% conifer and 20–71% hardwood cover. The average percent cover of hardwood across the eight sites in our study area was higher than around Great Gray Owl nests elsewhere in California (Wu et al. 2015), reflecting the overall greater abundance of oak trees in lower-montane forests of the Sierra Nevada than at higher elevations.

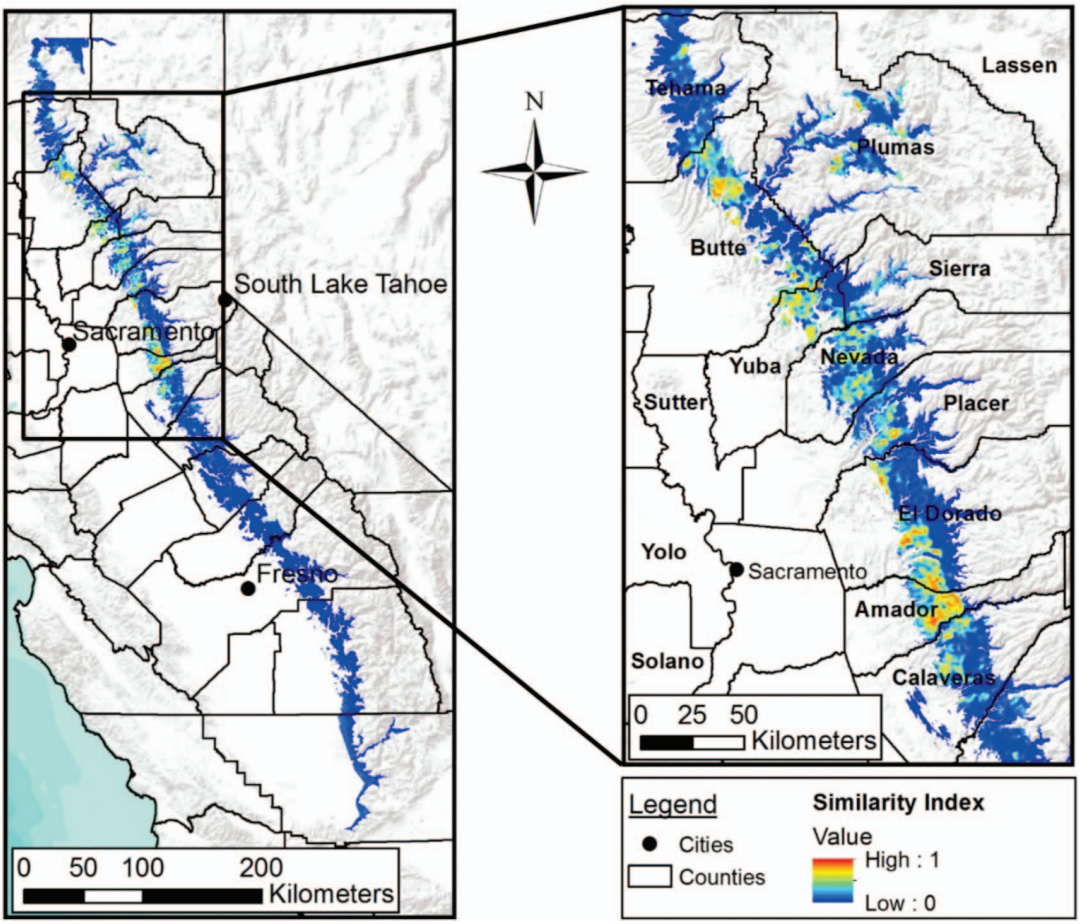

Figure 4. Maxent-generated index of similarity with Great Gray Owl nesting habitat at our study site, projected across the lower-montane zone of the Sierra Nevada.

Great Gray Owl nests were typically surrounded by dense forest (>60% canopy closure), consistent with findings from elsewhere in California (Greene 1995, Wu et al. 2015), Oregon (Bull and Henjum 1990), and eastern Idaho and northwest Wyoming (Whitfield and Gaffney 1997). More surprising was that the forests in a 900-m radius around nests contained large areas (109–204 ha) dominated by small-diameter trees (25.4–50.6 cm), whereas other research in California, based primarily on mid-elevation nest sites, has emphasized the importance of large trees in mid- to late-seral nest stands (Winter 1986, Sears 2006, Wu et al. 2015). In northeastern Oregon, Bull and Henjum (1990) found Great Gray Owls nesting in large trees in relatively late-seral stands, whereas in southwestern Oregon, areas around Great Gray Owl nests were characterized by a high number of small trees and low densities of large trees (Fetz et al. 2003), similar to what we observed at our study site. The fact that Great Gray Owls do not construct their own nests may limit their selection of nest stands to those that harbor appropriate nest structures (Bull and Henjum 1990), which could explain the wide range of nest-stand conditions Great Gray Owls use in and outside of California.

Stand structure at our study site was heavily influenced by shelterwood removal cuts that occurred primarily from 2005–2009, yielding early-seral forest conditions. Nevertheless, nest trees were uniformly large, with an average dbh of 102.5 cm. Thus, although it is unclear whether the abundance of small-diameter trees actually enhanced habitat for the owls or merely did not prevent them from using it, large oak trees (both dead and alive) clearly play a crucial role as nest trees in the lower-montane zone. Furthermore, selective retention of large conifers may also be important for supporting Great Gray Owls nesting in lower-montane forests. SPI has established an oak retention and recruitment management strategy that retains some oak trees and regenerates others by allowing natural seeds to germinate and grow or by replanting new seedlings during harvests. We urge other land managers throughout the lower-montane zone of the Sierra Nevada to retain large oaks as well as large, deteriorating trees of other species and encourage oak recruitment wherever possible. Where forest management practices or other factors have made suitable nesting opportunities rare, land managers should consider topping large snags to create nesting opportunities in broken-top snags.

Another surprising characteristic of the nest sites in our study area was their considerable distance from montane meadows. Previous work assessing habitat around mid-elevation Great Gray Owl nests has emphasized the importance of proximity to sufficiently large (~10 ha) wet meadows (Winter 1986, Greene 1995, van Riper and van Wagtendonk 2006, van Riper et al. 2013). In Yosemite National Park, nests average 80 m from meadows (Wu et al. 2015). The nests we studied ranged from 8–12 km from wet meadows, but were commonly <150 m from grassy openings (including herbaceous understory within oak riparian zones, roadside areas, comparatively dry lava cap meadows, plantations with wide spacing between trees, and oak savannah) that Great Gray Owls may be using for hunting in place of wet meadows. Characteristics of grassy openings, such as size, configuration, species composition, and grass height, that may support Great Gray Owl foraging in the lower-montane zone warrant further study.

Although our habitat assessment around Great Gray Owl nests was based primarily on remotely sensed data, those variables we assessed were highly correlated with field measures collected around nests, confirming the remotely sensed data reliably described conditions within our study area. However, it is possible that owls do not use the habitats around nests in proportion to their availability, or that some nests may be located near the edge of territories, such that the owls use areas well beyond the 900-m-radius plot we evaluated. Additional research on home-range sizes and resource use by Great Gray Owls in lower-montane forest could help resolve this issue.

Potential Nesting Habitat Elsewhere in the Lower-montane Zone. Further surveys of potential habitat within the lower-montane zone are needed to determine whether the cluster of territories at our study site indicates a highly restricted distribution of breeding owls within a small portion of the zone, or instead simply reflects very limited sampling effort devoted to this rather cryptic species. Our model of potential Great Gray Owl nesting habitat in the lower-montane zone of the Sierra Nevada suggests that relatively flat terrain (<15% slope) within dense, early-seral forest, comprising a combination of coniferous and hardwood species that also contains some large-diameter trees, was important for nesting habitat in our study area. Our model AUC of 0.963 indicates that the model was very effective at classifying presences and absences based on the data, likely reflecting the high similarity in habitat characteristics among the eight nesting territories.

Two of the most important variables in our model, dense canopy cover and relatively flat terrain, were consistent with previous knowledge about Great Gray Owl nesting habitat in the Sierra Nevada. (Winter 1986, Jepsen et al. 2011, Wu et al. 2015). However, two other important variables in our model, small-tree cover and large-tree cover, were more surprising, given that past work on Great Gray Owl habitat selection in the mid-elevation zone has emphasized the importance of large trees and late-seral characteristics (Winter 1986, Sears 2006, Wu et al. 2015). Contrary to our expectations, our similarity index identified landscapes with a high proportion of stands dominated by small trees, and a low proportion of stands dominated by large trees. Because we focused our study on heavily managed commercial forest, it remains unclear which habitat characteristics Great Gray Owls prefer in the lower montane zone. There may be aspects of early-seral commercial timberlands in this elevation zone that, in themselves, are attractive to Great Gray Owls, such as possible foraging opportunities found in plantation settings. Alternatively, Great Gray Owls may prefer less-managed later seral stage forest or other habitat types that we did not evaluate in this study. Land managers should survey low-elevation areas beyond our model predictions because of this uncertainty; our model simply provides a starting point.

Great Gray Owls with young (but without known nest sites) have also been recorded elsewhere at relatively low elevations in the central Sierra Nevada in recent years, in habitat similar to our study area (K. Roberts unpubl. data). These additional observations confirm that the species at least occasionally breeds in other areas within the lower-montane zone, though how commonly remains unknown. Our model identified areas within 10 counties near and north of our study area (in El Dorado County) that have habitat characteristics similar to our study area. It was unclear why nearly all of the areas identified by the model lay north of our study area, whereas the center of Great Gray Owl's range in California, at least in the mid-elevation zone, lies to the south, in and around Yosemite National Park. If more nest sites in the lower montane zone of the southern Sierra Nevada are discovered, additional modeling efforts should be undertaken to characterize habitat at those sites and then use those data to make our model more robust or to develop a separate model for identifying potential habitat south of our study area.

Our model has important limitations, including being based on a small sample of nest locations in a concentrated area that were found during surveys targeting habitat similar to that of the first nest discovered in our study area. Furthermore, the model does not consider ecological factors such as prey availability and interspecific competition. Nevertheless, we suggest that it is a useful tool for guiding initial survey efforts in portions of the lower-montane zone of the Sierra Nevada that have never been surveyed for Great Gray Owl. We recommend that areas identified as having a similarity index of >0.60 be prioritized for occupancy surveys, as they could potentially harbor undetected populations of this endangered species (to facilitate survey efforts, geospatial files indicating the precise locations of these areas are available from the authors), but that managers expand surveys beyond these areas when possible. We believe this threshold provides a good starting point for guiding new surveys because it strikes an appropriate balance between including areas that are similar to our study area while still likely yielding a relatively circumscribed target area that could realistically be surveyed with a reasonable expenditure of effort.

A final remaining question is whether Great Gray Owls historically nested in lower-montane forest, including our study area, or rather if their discovery in 2006 reflected recent colonization by the species. If Great Gray Owls only recently expanded their range downslope in the Sierra Nevada, it would provide an interesting counterexample to the more common phenomenon of montane species' ranges contracting or shifting upslope in response to climate change (Root et al. 2003, Parmesan 2006; but see also Tingley et al. 2012). Alternately, if Great Gray Owls were indeed present in the area long before their recent discovery, that would seem to bolster the possibility that there could be substantial numbers of Great Gray Owls elsewhere in the lower-montane zone that have not yet been detected. Those owls, at the lower margin of the species' elevation range, may be highly vulnerable to climate change; indeed the Great Gray Owl has been identified as one of 17 bird species in the Sierra Nevada with at least moderate vulnerability to climate change (Siegel et al. 2014). Understanding the species' distribution, ecology, and conservation needs at the lower extreme of its elevation range in California should be considered a high priority, as this may be the first segment of the population to be at serious risk due to climate change.

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LITERATURE CITED

ANGERT, A.L. AND D.W. SCHEMSKE. 2007. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* 59:1671–1684.

ARAÚJO, M.B. AND M. NEW. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22:42–47.

ARNAUD-HAOND, S., S. TEIXEIRA, S.I. MASSA, C. BILLOT, P. SAENGER, G. COUPLAND, C.M. DUARTE, AND E.A. SERRÃO. 2006. Genetic structure at range edge: low diversity and high inbreeding in Southeast Asian mangrove (*Avicennia marina*) populations. *Molecular Ecology* 15:3515–3525.

BATEMAN, B.L., A.M. PIDGEON, V.C. RADELOFF, A.J. ALLSTADT, H.R. AKÇAKAYA, W.E. THOGMARTIN, S.J. VAVRUS, AND P.J. HEGLUND. 2015. The importance of range edges for an irruptive species during extreme weather events. *Landscape Ecology* 30:1095–1110.

BECK, T.W. AND J. WINTER. 2000. Survey protocol for the Great Gray Owl in the Sierra Nevada of California. U.S.D.A. Forest Service, Vallejo, CA U.S.A.

BULL, E.L. AND J.R. DUNCAN. 1993. Great Gray Owl (*Strix nebulosa*). *In* A. Poole [ED.], The birds of North America online, No. 41. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/041 (last accessed 5 March 2015).

——— AND M.G. HENJUM. 1990. Ecology of the Great Gray Owl. U.S.D.A. Forest Service Gen. Tech. Rep. PNW-GTR-265, Portland, OR U.S.A.

CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE, NATURAL DIVERSITY DATABASE (CNDDB). 2015. State and federally listed endangered and threatened animals of California. http://www.dfg.ca.gov/biogeodata/cnddb/plants_and_animals.asp (last accessed 8 September 2015).

CALVEG. 2009. Existing vegetation – CALVEG. U.S. Forest Service, Pacific Southwest Region, McClellan, CA, U.S.A. http://www.fs.usda.gov/main/r5/landmanagement/gis (last accessed 20 August 2015).

ELITH, J., C.H. GRAHAM, R.P. ANDERSON, M. DUDIK, D. FERRIER, A. GUISAN, R.J. HIJMANS, F. HUETTMAN, J.R. LEATHWICK, A. LEHMANN, J. LI, L.G. LOHMANN, B.A. LOISELLE, G. MANION, C. MORITZ, M. NAKAMURA, Y. NAKAZAWA, J.M. OVERTON, A.T. PETERSON, S.J. PHILLIPS, K. RICHARDSON, R. SCACHETTI-PEREIRA, R.E. SCHAPIRE, J. SOBERON, S. WILLIAMS, M.S. WISZ, AND N.E. ZIMMERMANN. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.

ESRI. 2014. ArcGIS Desktop: Release 10.3 Environmental Systems Research Institute, Redlands, CA U.S.A.

EVANS, J.S., J. OAKLEAF, S.A. CUSHMAN, AND D. THEOBALD. 2014. An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0-0. http://evansmurphy.wix.com/evansspatial (last accessed 26 January 2015).

FETZ, T.W., S.W. JANES, AND H. LAUCHSTEDT. 2003. Habitat characteristics of Great Gray Owl sites in the Siskiyou Mountains of southwestern Oregon. *Journal of Raptor Research* 37:315–322.

FRANKLIN, A.B. 1988. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. *Condor* 90:689–696.

FRANKLIN, J. AND J.A. MILLER. 2009. Mapping species distributions: spatial inference and prediction. Cambridge Univ. Press, Cambridge, U.K.

FRYJOFF-HUNG, A. AND J. VIERS. 2012. Sierra Nevada Multi-Source Meadow Polygons Compilation, version 1.0. Center for Watershed Sciences, University of California Davis, Davis, CA U.S.A. http://meadows.ucdavis.edu (last accessed 20 August 2015).

GASTON, K.J. 2003. The structure and dynamics of geographic ranges. Oxford Univ. Press, New York, NY U.S.A.

GREENE, C. 1995. Habitat requirements of Great Gray Owls in the central Sierra Nevada. M.S. thesis, University of Michigan, Ann Arbor, MI U.S.A.

GRIFFITH, T.M. AND M.A. WATSON. 2006. Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *American Naturalist* 167:153–164.

HOLT, R.D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5:159–178.

HOPKINS, A.D. 1938. Bioclimatics; a science of life and climate relations. U.S. Department of Agriculture Misc. Publ. 280, Washington, DC U.S.A.

HULL, J.M., A. ENGILIS, JR., J.R. MEDLEY, E.P. JEPSEN, J.R. DUNCAN, H.B. ERNEST, AND J.J. KEANE. 2014. A new subspecies of Great Gray Owl (*Strix nebulosa*) in the Sierra Nevada of California, U.S.A. *Journal of Raptor Research* 48:68–77.

———, J.J. KEANE, W.K. SAVAGE, S.A. GODWIN, J.A. SHAFER, E.P.B. JEPSEN, R. GERHARDT, C. STERMER, AND H.B. ERNEST. 2010. Range-wide genetic differentiation among North American Great Gray Owls (*Strix nebulosa*) reveals a distinct lineage restricted to the Sierra Nevada, California. *Molecular Phylogenetics and Evolution* 56:212–221.

JEPSEN, E.P.B., J.J. KEANE, AND H.B. ERNEST. 2011. Winter distribution and conservation status of the Sierra Nevada Great Gray Owl. *Journal of Wildlife Management* 75:1678–1687.

KAWECKI, T.J. 2008. Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics* 39:321–342.

KEANE, J.J., H.B. ERNEST, AND J.M. HULL. 2011. Conservation and management of the Great Gray Owl 2007–2009: Assessment of multiple stressors and ecological limiting factors. National Park Service and U.S.D.A. Forest Service Interagency Report F8813-07-0611, Davis, CA U.S.A.

MACKENZIE, D.I., J.D. NICHOLS, J.E. HINES, M.G. KNUTSON, AND A.B. FRANKLIN. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.

MANEL, S., H.C. WILLIAMS, AND S.J. ORMEROD. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.

MAYER, K.E. AND W.F. LAUDENSLAYER [EDS.]. 1988. A guide to wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento, CA U.S.A.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.

PEARSON, R.G., C.J. RAXWORTHY, M. NAKAMURA, AND A. TOWNSEND PETERSON. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102–117.

PHILLIPS, S.J., R.P. ANDERSON, AND R.E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.

——— AND M.K. DUDIK. 2008. Modeling of species distributions with MAXENT: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.

———,———, AND R.E. SCHAPIRE. 2010. Maxent Software, version 3.3. http://www.cs.princeton.edu/~schapire/maxent/ (last accessed 6 July 2015).

ROOT, T.L., J.T. PRICE, K.R. HALL, S.H. SCHNEIDER, C. ROSENZWEIG, AND J.A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.

SAMIS, K.E. AND C.G. ECKERT. 2009. Ecological correlates of fitness across the northern geographic range limit of a Pacific Coast dune plant. *Ecology* 90:3051–3061.

SEARS, C. 2006. Assessing distribution, habitat suitability, and site occupancy of Great Gray Owls (*Strix nebulosa*) in California. M.S. thesis, University of California, Davis, CA U.S.A.

SEXTON, J.P., P.J. MCINTYRE, A.L. ANGERT, AND K.J. RICE. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.

SIEGEL, R.B., P. PYLE, J.H. THORNE, A.J. HOLGUIN, C.A. HOWELL, S. STOCK, AND M. TINGLEY. 2014. Vulnerability of birds to climate change in California's Sierra Nevada. *Avian Conservation and Ecology* 9:7.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pages 157–170 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. National Wildlife Federation, Washington, DC U.S.A.

SWETS, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285.

TINGLEY, M.W., M.S. KOO, C. MORITZ, A.C. RUSH, AND S.R. BEISSINGER. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* 18:3279–3290.

U.S. FOREST SERVICE. 2013. Natural Resource Information System (NRIS), Natural Resource Manager. http://www.fs.fed.us/nrm/index.shtml (last accessed 23 April 2014).

VAN RIPER, C., III, J.J. FONTINE, AND J.W. VAN WAGTENDONK. 2013. Great Gray Owls (*Strix nebulosa*) in Yosemite National Park: on the importance of food, forest structure, and human disturbance. *Natural Areas Journal* 33:286–295.

——— AND J. VAN WAGTENDONK. 2006. Home range characteristics of Great Gray Owls in Yosemite National Park, California. *Journal of Raptor Research* 40:130–141.

WISZ, M.S., R.J. HIJMANS, J. LI, A.T. PETERSON, C.H. GRAHAM, A. GUISAN, AND NCEAS PREDICTING SPECIES DISTRIBUTIONS WORKING GROUP. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763–773.

WHITFIELD, N.B. AND M. GAFFNEY. 1997. Great Gray Owl habitat use within altered forest landscape. Pages 498–505 *in* J.R. Duncan, D.H. Johnson, and T.H. Nicholls [EDS.], Biology and conservation of owls of the Northern Hemisphere. U.S.D.A. Forest Service Gen. Tech. Rep. NC-190, Fort Collins, CO U.S.A.

WINTER, J. 1980. Status and distribution of the Great Gray Owl in California. State of California Department of Fish and Game Project W-54-R-12, Sacramento, CA U.S.A.

———. 1986. Status, distribution, and ecology of the Great Gray Owl (*Strix nebulosa*) in California. M.S. thesis, San Francisco State University, San Francisco, CA U.S.A.

WU, J.X., R.B. SIEGEL, H.L. LOFFLAND, M.W. TINGLEY, S.L. STOCK, K.N. ROBERTS, J.J. KEANE, J.R. MEDLEY, R. BRIDGMAN, AND C. STERMER. 2015. Diversity of Great Gray Owl nest sites and nesting habitats in California. *Journal of Wildlife Management* 79:937–947.

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