RARITY OF SPOTTED OWLS IN SOUTHERN CALIFORNIA

JOSHUA M. BARRY,* GAVIN M. JONES, BENJAMIN ZUCKERBERG, RICHARD TANNER, NICHOLAS F. KRYSHAK, AND M. ZACHARIAH PEERY

Department of Forest and Wildlife Ecology, University of Wisconsin–Madison, Madison, WI 53706 (JMB, BZ, NFK, MZP)
United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Albuquerque, NM 87102 (GMJ)
Tanner Environmental Services, Alameda, CA 94501 (RT)
**Correspondent: jmbarry3@wisc.edu*

ABSTRACT—The California spotted owl (*Strix occidentalis occidentalis*), an older forest species of conservation concern, has declined in many historically occupied forests due to habitat loss from severe wildfire and other environmental changes. Although population trends have been well documented in the Sierra Nevada mountain range in the western United States, less is known about population status at the range boundary in Southern California, a region experiencing rapid environmental change. Therefore, we conducted extensive spotted owl nighttime surveys during the 2022 breeding season in the San Gabriel Mountains of the San Bernardino and Angeles national forests, the Sierra Pelona Mountains of the Angeles National Forest, and the Los Padres National Forest. These surveys included historically occupied territories; spatially extensive, low-intensity surveys outside of these historical territories; and surveys in regions with potentially high-quality owl habitats. We compared remotely sensed data of vegetation conditions and disturbance between currently occupied and currently vacant territories, and at currently vacant territories during the period of historical occupancy and after the loss of territorial owls, to assess potential causes of population change. We made 1,913 visits to call points, surveying an area of 1,100 km^2, yet we located only eight currently occupied territories. Out of 13 historically occupied territories, only 3 (23%) remained occupied. Currently, spotted owls were more likely to occupy territories with a greater basal area of deciduous trees. Furthermore, currently vacant territories had greater levels of drought-related tree mortality after the period of detection of the last owls. Our findings suggest that habitat scarcity, exacerbated by drought-induced tree mortality, declines in oaks, and possibly warming temperatures, may be contributing to spotted owl population declines in Southern California, although the small number of occupied territories in the region limited inferences. Our results align with other recent work indicating this species' rarity and decline in Southern California, with functional but declining populations in the San Bernardino Mountains.

RESUMEN—El búho moteado de California (*Strix occidentalis occidentalis*) – una especie forestal antigua de interés para la conservación – ha disminuido en muchos bosques ocupados históricamente debido a la pérdida de hábitat por los graves incendios forestales y otros agentes de cambio que han afectado a la vegetación. A pesar de que las tendencias poblacionales de los búhos y los factores responsables por esas tendencias han sido bien estudiados en la cordillera de Sierra Nevada en el oeste de Estados Unidos, se sabe menos sobre el estado de la población en el límite del área de distribución en el sur de California, una región que está experimentando un rápido cambio medioambiental. Por lo tanto, realizamos estudios nocturnos extensos del búho moteado durante la temporada de reproducción del 2022 en las Montañas de San Gabriel de los Bosques Nacionales de San Bernardino y Angeles, las Montañas de Sierra Pelona del Bosque Nacional de Angeles, y dentro el Bosque Nacional de Los Padres. Estos estudios incluyeron estudios enfocados en los territorios que han sido históricamente ocupados por búhos moteados; estudios espacialmente extensos y de baja intensidad fuera de los territorios que han sido históricamente ocupados; y estudios en áreas específicamente escogidas por su habitat de potencialmente alta calidad para los búhos moteados. Como análisis exploratorio, usamos datos de teledetección para comparar las perturbaciones y las condiciones de la vegetacion entre los territorios que están actualmente ocupados y los que están actualmente desocupados. Para comprender las causas del cambio poblacional, también comparamos datos obtenidos mediante detección remota sobre las condiciones de la vegetación y las perturbaciones entre territorios actualmente ocupados y actualmente vacantes, y en territorios actualmente vacantes durante el período de ocupación histórica y después de la pérdida de los búhos territoriales. Realizamos 1,913 visitas a los puntos de llamada, inspeccionando un área de aproximadamente 1,100 km^2, aunque sólo localizamos ocho territorios actualmente ocupados. De los 13 territorios que fueron históricamente ocupados, sólo 3 (23%) permanecían ocupados. En la actualidad, es más probable que los búhos moteados ocupen territorios con mayor área basal de árboles caducifolios. Además, los territorios que están actualmente desocupados presentaban mayores niveles de mortalidad arbórea relacionada con la sequía después del periodo de detección de los últimos búhos.

Así pues, además de la escasez de hábitat adecuado, la rareza y posible pérdida de territorios que observamos en esta región puede estar relacionada con el declive de los robles y la mortalidad de los árboles porla sequía, potencialmente en conjunto con el calentamiento de las temperaturas, aunque el pequeño número de territorios ocupados en la región limitó nuestras inferencias. Nuestros resultados son consistentes con otros estudios recientes que indican que los búhos moteados parecen ser raros o estar en declive en muchas partes del sur de California, con poblaciones funcionales pero en declive en las montañas de San Bernardino.

The spotted owl (*Strix occidentalis*) is an older forest species native to western North America. There have been declines in spotted owl populations in many forests throughout their range because of extensive severe wildfires (Jones et al., 2021), loss of large trees (Jones et al., 2018), fire suppression (Collins et al., 2017; Hobart et al., 2019; Kramer et al., 2021), and competition with invasive barred owls (*Strix varia*; Diller et al., 2016; Wiens et al., 2021). The combination of ever-evolving factors threatening spotted owl populations has had significant implications for the conservation of this species, and subsequently the management of many forests in western North America, for nearly 4 decades (Verner et al., 1992).

The northern spotted owl (*Strix occidentalis caurina*) and the Mexican spotted owl (*Strix occidentalis lucida*) subspecies are currently on the list as "threatened" under the Endangered Species Act (United States Fish and Wildlife Service, 1990, 1993). By contrast, the California spotted owl (*Strix occidentalis occidentalis*) subspecies, distributed in the Sierra Nevada mountain range in the western United States, southern Coast Range, and interior mountains of Southern California, is not currently on the list under the Endangered Species Act. However, following multiple petition attempts, the United States Fish and Wildlife Service (2023) proposed listing the Coastal Southern California distinct populations as endangered and listing the Sierra Nevada populations as threatened (88 FR 11600). There is increasing concern over the status of California spotted owls in recent years because of declining populations in the Sierra Nevada (Conner et al., 2013, 2016; Tempel et al., 2014*a*), the core of the subspecies range. Although study of the trends and factors responsible for changes in California spotted owl populations is comprehensive in the Sierra Nevada, less is known about their population status in the southern interior regions of Southern California.

The California spotted owl occurs primarily in four national forests in Southern California (Gutiérrez et al., 2017; Fig. 1), where in general there is isolation of populations across forests because the distance between mountain ranges often exceeds dispersal distance (Lahaye et al., 1994, 2001). The San Bernardino Mountains in the San Bernardino National Forest harbor the largest owl populations in Southern California (LaHaye et al., 1992; Gutiérrez et al., 2017). Franklin et al. (2004) did not detect population declines in the San Bernardino Mountains from 1992 to 1998 by using mark–recapture methods, but LaHaye et al. (2004) found a 9% annual decline from 1987 to 1998 by using a matrix modeling approach. More recently, Tempel et al. (2022) showed a decline in the mean occupancy rate of spotted owl territories in the San Bernardino and San Jacinto mountains, also in the San Bernardino National Forest, from 0.82 in 1991 to 0.39 in 2019. In the Palomar Mountains of the Cleveland National Forest, spotted owls once occurred at high densities, particularly in isolated, forested canyons (Gutiérrez and Pritchard, 1990). Since then, there has been a decline in naïve occupancy rate in the Cleveland National Forest from 0.52 in 1991 to 0.11 in 2020 (Tempel et al., 2022). However, in the Los Padres and Angeles national forests, little is known about the current population status of California spotted owls because of lack of systematic widescale survey efforts for nearly 2 decades.

The goals of our study were to 1) better understand the status of California spotted owl territory occupancy in areas of Southern California with less extensive surveys and 2) explore potential environmental factors (i.e., vegetation conditions and disturbance history) responsible for potential changes in spotted owl populations in these areas. To do so, we conducted three types of spotted owl surveys from March to August 2022 in the San Gabriel Mountains of the San Bernardino and Angeles national forests, the Sierra Pelona Mountains of the Angeles National Forest, and throughout the Los Padres National Forest: 1) surveys focused within historically occupied territories; 2) spatially extensive, low-intensity surveys outside of historically occupied territories; and 3) targeted surveys in areas consisting of potentially high-quality owl habitat (i.e., big trees and large amounts of canopy cover). We designed our surveys to determine naïve occupancy status at historical territories and to locate owls across a broad gradient of ecological conditions known to constitute suitable owl nesting and roosting habitat in the area, before the implementation of fuel reduction programs, and to inform the current Endangered Species Act listing decision.

Materials and Methods—*Study Area*—Our study area encompassed ~1,100 km^2 of public land in the Los Padres, Angeles, and San Bernardino national forests, California, during the 2022 summer breeding season (Fig. 1). The area included topographically complex mountain ranges that vary in elevation, vegetation type, and climatic conditions. The climate was Mediterranean, and most precipitation occurred from December to February (winter) as rain or snow. Elevations ranged from ~500 to 3,100 m. At lower elevations, shrubland and chaparral was the common ground cover, interspersed with deciduous forest. Common deciduous species included white alder (*Alnus rhombifolia*), black cottonwood (*Populus trichocarpa*), Fremont cottonwood (*Populus fremontii*), western sycamore (*Platanus racemosa*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*), with California black oak exhibiting relatively high fire resilience (i.e., steams typically resprout

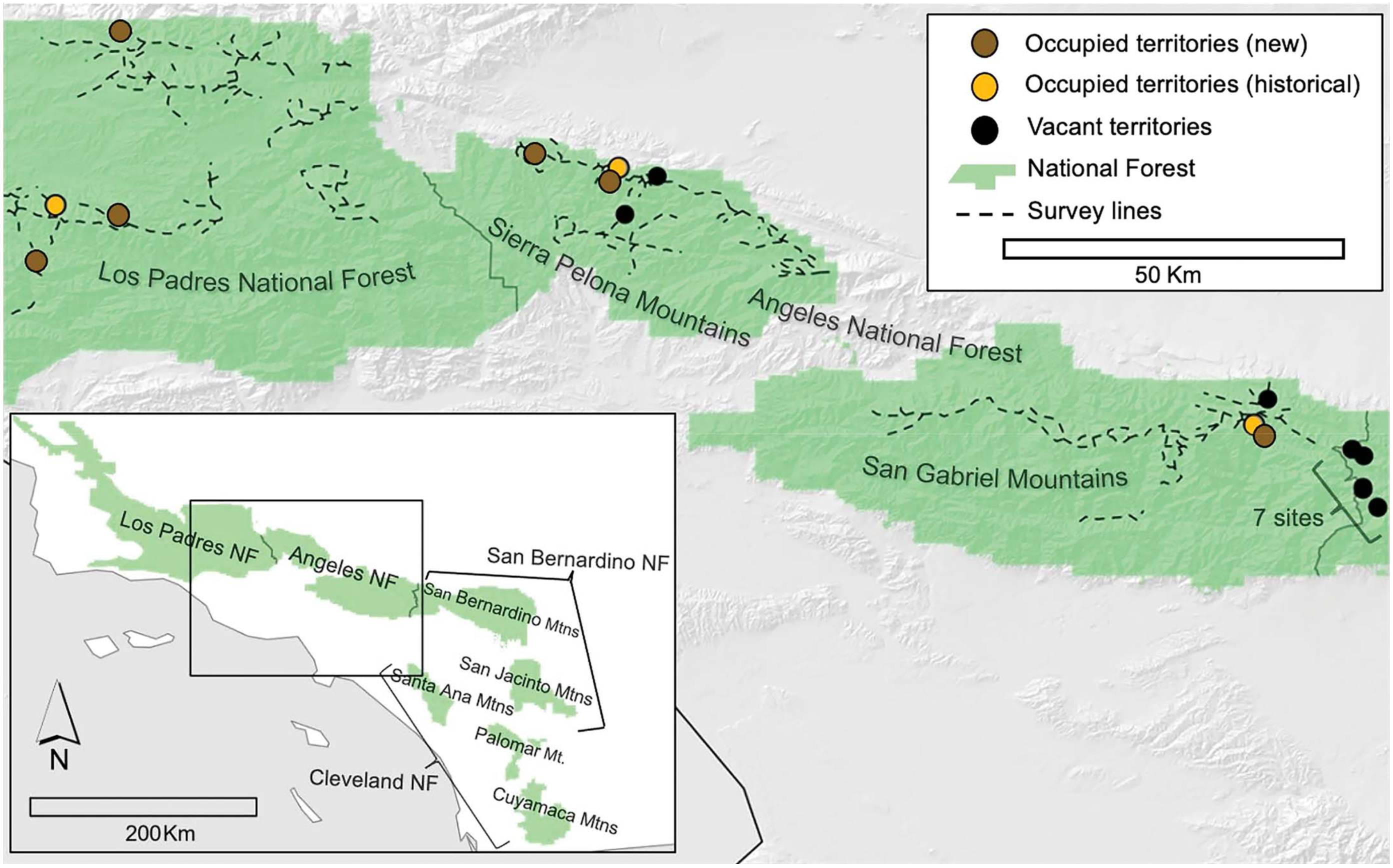

Fig. 1—Study area in the Los Padres, Angeles, and San Bernardino national forests in California, USA, with the locations of occupied spotted owl territories identified during our 2022 field surveys (orange and brown dots), as well as currently vacant territories (black dots) ranging from 1990 to 2011 since the detection of the last spotted owl in these areas.

immediately following wildfire; Cocking et al., 2012). Conifer forests occurred at higher elevations on north-facing slopes and in canyon bottoms, with common species including Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Coulter pine (*Pinus coulteri*), white fir (*Abies concolor*), and big-cone Douglas fir (*Pseudotsuga macrocarpa*). Great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), and red-tailed hawks (*Buteo jamaicensis*) were the main predators of spotted owls (Gutiérrez et al., 1995). The dusky-footed woodrat (*Neotoma fuscipes*) and Botta's pocket gopher (*Thomomys bottae*) were the primary prey species (Smith et al., 1999). Spotted owls in Southern California are found in high-elevation forests above the less suitable shrub and semiarid vegetation zones at lower elevations and in canyon bottoms at lower elevations with deciduous and coniferous trees. As such, suitable owl habitat is typically discontinuous and appears to result in isolated owl populations without known dispersal between mountain ranges (Noon and McKelvey, 1992; Lahaye et al., 2001; LaHaye and Gutiérrez, 2005).

Spotted Owl Surveys—We conducted spotted owl surveys from mid-March to mid-August 2022. The time frame of our study corresponded with the breeding season of spotted owls and therefore increased the likelihood of finding offspring and nesting sites. As part of our first survey method, we surveyed 13 historically occupied territories during the period 1990–2011 in the Los Padres ($n = 1$), Angeles ($n = 5$), and San Bernardino ($n = 7$) national forests (Fig. 1). We used this time frame because these were the only territories with historical data on daytime roosting and nesting sites, with limited surveys in the Angeles and Los Padres national forests during the 21st century. All the territories surveyed in the San Bernardino National Forest were in the San Gabriel Mountains near the border of the Angeles National Forest (Fig. 1). We did not survey three historical territories for safety concerns. We surveyed historically occupied territories by visiting eight call points at and around the center of the historical territory (i.e., historical daytime roost or nest location), representing the number of call points that a team of two technicians could complete in one night. We spaced call points by 200–400 m in topographically advantageous locations to maximize broadcast coverage. If two historical territories were within 400 m of each other, we surveyed them as a group (i.e., eight total call points around both territories). We surveyed individual call points for 10 min in the twilight and nighttime hours. We visited call points twice, with the first and second visits separated by 1 mo unless owls were found as part of the first visit. During our surveys, we had a person mimic the territorial four-note calls of spotted owls and record any responses from the owls as we surveyed at designated call points and while traveling between them (Forsman, 1983). If we did not visually detect an owl after two visits, we classified the territory as vacant. In cases where we visually or audibly detected a spotted owl at night, we conducted dawn, diurnal, and twilight walk-in surveys on the following day. We did so because spotted owls are known to roost within their resident nest-roost during diurnal hours, indicating territory occupancy (Berigan et al., 2019). If we detected an owl audibly, but not visually, we considered the site occupied but excluded it from our statistical analyses. If we visually detected an owl roosting or nesting, we classified the territory as occupied.

As part of our second survey method, we surveyed areas outside of historically occupied territories and conducted spatially extensive, low-intensity surveys to find owl territories across a broad ecological gradient known to constitute suitable owl habitats. We used two sources of information to create call point locations. First, we compiled a list of historical spotted owl detections from 1986 to 2021 by using the California Natural Diversity Database, an inventory of the status and locations of rare plants and animals in California. Historical spotted owl detections in the California Natural Diversity Database primarily consisted of nighttime observations by United States Forest Service personnel or biologists. We prioritized call point locations in areas with no or few historical survey efforts (less than or equal to two visits at a call point in an area) and excluded areas with a historical nest or roost site, which we included as part of our first survey method. On a few occasions, surveys overlapped with a historical roost or nest site because of limited amounts of suitable owl habitat. We separated potential call points by 1,000 m to cover a spatially expansive survey area and placed call points on national forest roads and trails and in acoustically advantageous areas, such as ridge tops. Second, we overlayed 2017 Gradient Nearest Neighbor (GNN; LEMMA Lab, Oregon State University, Corvallis, Oregon, USA) maps of forest structure on top of our potential call point locations. GNN interpolates information from forest inventory plots by using Landsat satellite imagery (30-m resolution). GNN maps were available each year from 1986 to 2017. We calculated mean vegetation conditions—including basal area of live coniferous and deciduous trees (≥2.5-cm diameter at breast height) and percent canopy cover—in a 1,000-m radius buffer at each call point by using 2017 GNN forest structure maps.

Next, we grouped call points spatially close to one another into survey polygons for logistical purposes. We then designated polygons as high ($n = 6$) or low ($n = 4$) priority based on the mean vegetation conditions inside each polygon (Fig. S1). Low-priority polygons had similar vegetation conditions and relatively low habitat quality (i.e., more shrubland and open areas with low tree densities). High-priority polygons had a wide range of habitat conditions suitable for owls and higher habitat quality (i.e., more forested habitat with medium-to-large trees) than low-priority polygons. The average number of call points at a high-priority polygon was 194, and the average spatial coverage of a high-priority polygon was 235 km^2. We then divided polygons into survey groups that had ~30 call points, representing the number of call points that a team of two technicians could complete in a survey visit in 48 h. We surveyed 58 survey groups twice during the field season (Fig. S2), with visits separated by an average of 40 days (5th quantile, 6 days; 95th quantile, 82 days). We surveyed 9 of the 58 survey groups twice in a relatively short period (i.e., <3 wk between visits), which reflected a small number of territories that were accessible during the springtime because of snow and windstorms at medium-to-high elevations. We prioritized surveys in high-priority areas and conducted surveys in low-priority areas after completion of surveys in high-priority areas. Similar to our first survey methods, we surveyed individual call points twice for 10 min, with the first and second visits separated by 1 mo unless owls were found as part of the first visit. We chose a two-visit protocol instead of the traditional six-visit approach used in demographic studies to maximize our spatial coverage and potentially locate owls in different areas across the national forests. If we visually detected an owl, we classified the roosting-nesting location as the center of the currently occupied territory. In cases where we visually or audibly detected a spotted owl at night, we conducted dawn, diurnal, and twilight walk-in surveys on the following day.

For our third survey method, we conducted nighttime spotted owl surveys in areas considered to have high-quality habitat or potential spotted owl habitat within or immediately adjacent to proposed fuel reduction programs across the Los Padres and Angeles national forests. Similar to our other survey methods, we conducted these surveys in the Los Padres and Angeles national forests during the spotted owl breeding season. We visited call points three times for ~10 min on each visit, with visits separated by ~1 mo. We included data from all three survey methods in our analyses.

Testing for Change in Vegetation Conditions at Owl Territories—Two important goals of our study included identifying reasons for historically occupied territories potentially becoming vacant at any point between the period of last known historical occupancy and the 2022 surveys and comparing environmental conditions between occupied and vacant territories. In alignment with these goals, we conducted two primary analyses: 1) examining differences in the present vegetation conditions between currently occupied and vacant territories; and 2) for currently vacant territories with historical occupation, assessing differences in the vegetation conditions during the period of historical occupancy and after the presumed loss of territorial owls, as determined by the 2022 surveys.

We created a circular buffer with a 3,000-m radius centered at the roost-nest location of a territory, representing an area where multiple individual spotted owls could occur (Zimmerman et al., 2001). We chose this scale based on Tempel et al. (2022), who found this scale to be significant for predicting spotted owl occupancy rates in Southern California and because owls can travel relatively far distances. Next, we overlayed each buffer with present and historical GNN forest structure maps of basal area of coniferous and deciduous trees to calculate average vegetation estimates within those boundaries. Because the most recent GNN forest structure maps represented conditions in 2017, we tested for differences in two major causes of forest disturbance from 2018 to 2021 (see *Statistical Analyses* section). To determine the historical vegetation conditions of currently vacant territories, we used GNN forest structure maps from the initial year of territory occupancy and overlaid the territory buffer onto it and then we compared these historical conditions with the current vegetation conditions by overlaying 2017 forest structure maps in the same buffer. Finally, we compared the conditions of currently occupied territories with currently vacant territories by overlaying 2017 forest structure maps in their respective buffers.

Testing for Differences in Wildfire Disturbance at Owl Territories—We tested for differences in the cumulative amount of high-severity wildfire at occupied and vacant territories, and at vacant territories during the period of historical occupancy and after the loss of territorial owls, to understand potential causes of changes in occupancy due to forest disturbance. To do so, we gathered wildfire severity maps from the Monitoring Trends in Burn Severity database (i.e., 30 × 30 m; http://www.mtbs.gov/). Monitoring Trends in Burn Severity assesses burn area and severity from pre- and postdisturbance satellite imagery (Eidenshink et al., 2007) for large (>400-ha) wildfires. Monitoring Trends in Burn Severity calculates the differenced normalized burn ratio between imagery before the fire with imagery from up to a year later. For vacant territories, we created a static wildfire map by calculating the cumulative proportion of buffer area burned by high-severity wildfire starting from 2021 and going backward to the initial year of occupancy, as determined by previous surveys. This period represents the "present conditions" at currently vacant territories. To understand the "historical conditions" at these territories, we created a static map of the cumulative proportion of buffer area burned by high-severity wildfire for the same duration before the first year of known occupancy. On average, a territory remained vacant for 18 yr. Therefore, to represent present conditions at currently occupied territories, we calculated the high-severity wildfire over the past 20 yr (2001–2021), which is approximately the mean time a territory remained vacant.

Testing for Differences in Drought-Related Tree Mortality at Owl Territories—We also tested for differences in drought-related tree mortality at occupied territories and vacant territories, and at vacant territories during the period of historical occupancy and after the loss of territorial owls, to understand potential causes of change in occupancy. We obtained annual tree mortality maps at 30-m resolution from the Ecosystem Disturbance and Recovery Tracker, an image analysis system that processes historical Landsat imagery at a temporal accuracy of 8–16 days to detect ecosystem disturbances (Koltunov et al., 2020). The Ecosystem Disturbance and Recovery Tracker data provided temporal coverage spanning from 1998 to 2021. Disturbance events could be the result of a wide range of disturbance types and agents (Koltunov et al., 2020), including canopy removal or damage by human intervention (e.g., harvesting, mastication, thinning, selective logging, and prescribed burns), natural causes (e.g., blowdown, landslide, flood, wildfire), and rapid tree mortality (i.e., replacement of live leaves-trees with dead leaves-trees, irrespective of phenology), likely a result of drought- or insect-induced tree mortality. We excluded territories with wildfire during the year that these tree mortality disturbances occurred. We also used the Hazardous Fuel Treatment dataset of the United States Forest Service to overlay potential fuel treatments that had occurred within the territory boundaries. We limited fuel treatments to a few occupied territories, with these treatments mostly occurring within the 2020 Lake Fire perimeter following the fire. We used the Ecosystem Disturbance and Recovery Tracker data to create Mortality Magnitude Index maps for all years dating back to 1998, which included annual estimates of live canopy cover loss (percentage) at the pixel level (900-m^2 area). We then overlayed these maps with our vacant and occupied territory buffers to calculate average estimates of canopy cover loss within those boundaries. We quantified drought-related tree mortality in territory buffers for each year by summing the spatial area of all pixels identified as experiencing any (i.e., $>0\%$) canopy cover loss. Consequently, our estimate of drought-related tree mortality represented the spatial area, or proportional area, of territory buffers with drought-related tree mortality.

To determine the potential impact of drought-related tree mortality on occupancy, we compared the levels of such mortality between currently vacant territories and occupied territories. To do so, we overlayed annual Mortality Magnitude Index maps corresponding to each year with our vacant territory buffers from the period of historical occupancy to the presumed loss of territorial owls to 2021. Next, we calculated a mean annual tree mortality rate, represented by the average annual proportional area of territory buffer with any amount of canopy cover loss, for each vacant territory. We used this mean annual tree mortality rate, rather than the individual annual rates, in our final analysis. For comparison, we used the same approach to estimate drought-related tree mortality at occupied territories over 20 yr (2001–2021). Next, to assess the possible impact of drought-related tree mortality on territory vacancy, we investigated whether there were differences in such mortality at vacant territories during the period of historical occupancy compared with after the presumed loss of territorial owls up to 2021 (see *Statistical Analyses* section). To do so, we calculated a mean annual tree mortality rate at vacant territories for the same length of time before and after the initial year of historical occupancy.

Statistical Analyses—To assess potential differences in wildfire disturbance at vacant and occupied territories following the most up-to-date GNN forest structure maps of 2017, we compared the cumulative amount of high-severity wildfire activity from 2018 to 2021 by using an unpaired t test. In addition, we used the same statistical test to contrast the average annual tree mortality rates at vacant and occupied territories during the same period, aiming to identify potential disparities in recent drought-induced disturbances. Our findings indicated no significant differences in high-severity wildfire or drought disturbance between the two types of territories (Table S1), affirming the suitability of the 2017 vegetation metrics as representative of the conditions observed at territories during our 2022 surveys.

We used two sets of logistic regression models (Table 1) to investigate how vegetation structure and forest disturbance may have influenced territory occupancy. The first set compared present conditions at currently occupied (n = 8) and currently vacant (n = 10) territories, whereas the second set compared present (n = 10) and historical (n = 10) conditions at currently vacant territories. Because we conducted only two surveys per site and the number of occupied territories in the region was small, we did not use site occupancy models that account for imperfect detection and require estimating additional parameters. We recognize that detection probability can vary due to several factors, such as owl breeding status, but conducting more surveys per site was not feasible given the large area that we surveyed and the logistical constraints. Furthermore, estimates of survey-specific detection probabilities for California spotted owls in the central Sierra Nevadas are 0.50 for nonbreeding owls and 0.83 for breeding owls (Tempel et al., 2014*b*). These probabilities increase to 0.75 and 0.97 with two surveys per season and 0.87 and 0.99 with three surveys, respectively. Thus, we likely had a reasonable probability of detecting occupied territories.

We considered high-severity wildfire, basal area of deciduous trees, basal area of coniferous trees, percent canopy cover, and drought-related tree mortality as predictors in both sets of logistic regression models. To test for and remove collinearity among predictors, we calculated Pearson's correlation coefficient; this calculation led to the removal of percent canopy cover as a vegetation predictor due to its strong collinearity (r = 0.47–0.82) with other predictors. We z-standardized all of the predictors to ensure that they were on the same scale and to facilitate comparison of their effect sizes during the logistic regression analysis. To identify the most significant predictors, we initially evaluated each predictor individually by building separate models for each predictor and then calculating the corrected Akaike's Information Criterion (AICc) and AIC weight to assess their relative importance. Once we determined the top predictor by these metrics, we integrated it with the remaining covariates in the first set of logistic regression models. This method enabled us to identify potentially important predictors individually while considering the influence of other pertinent variables. Owing to challenges in parameter estimation and model convergence when incorporating multiple predictors in our second series of logistic regression models, we restricted each model to include only one predictor. We included a null model with no predictors in both sets of logistic regression models. To assess the relative support for different models, we used several

TABLE 1—Model comparison and model fit for all logistic models used to compare environmental conditions and disturbance at occupied and vacant spotted owl territories in Southern California, USA. We ranked models based on corrected Akaike's Information Criterion (ΔAICc), with w = AICc weight, K = number of parameters, $\log\mathscr{L}$ = log likelihood, and McFadden's pseudo-R^2 included.

Test	Model covariate(s)	AICc	ΔAICc	w	K	$-2\log\mathscr{L}$	McFadden's pseudo-R^2
Occupied vs. vacant (current conditions)	Deciduous trees	18.17	0.00	0.58	2	−6.68	0.46
	Deciduous + coniferous trees	21.04	2.88	0.14	3	−6.67	0.46
	Deciduous trees + high-severity fire	21.07	2.90	0.14	3	−6.68	0.46
	Deciduous trees + drought	21.08	2.91	0.13	3	−6.68	0.46
	Null	26.98	8.81	0.01	1	−12.37	NA[a]
	Coniferous trees	28.41	10.24	<0.01	2	−11.80	0.05
	High-severity fire	29.23	11.06	<0.01	2	−12.21	0.01
	Drought	29.51	11.34	<0.01	2	−12.36	<0.01
Within-vacant (current vs. historical conditions)	Drought	14.64	0.00	0.99	2	−4.89	0.58
	High-severity fire	27.11	12.46	<0.01	2	−11.20	0.19
	Null	29.95	15.31	<0.01	1	−13.86	NA
	Deciduous trees	31.29	16.64	<0.01	2	−13.29	0.04
	Coniferous trees	32.42	17.78	<0.01	2	−13.86	<0.01

[a] NA = not applicable.

metrics, including change in AICc (ΔAICc), AIC weight, and McFadden's pseudo-R^2. Specifically, we selected models that had a ΔAICc of <2 units compared with the top-ranked model (Burnham and Anderson, 2002). To evaluate the magnitude and certainty of the β coefficient estimates, we assessed whether their 85% confidence intervals overlapped with zero (Arnold, 2010).

RESULTS—We made 1,913 visits to 923 call points (Fig. 1): 64 visits as part of our survey efforts within historical territories (survey method 1); 1,561 visits as part of our spatially extensive survey design (survey method 2); and 288 visits as part of our targeted surveys in high-quality owl habitat (survey method 3). We visually located eight occupied territories, five by pairs and three by single owls. Of the eight occupied territories, four had roosting juveniles present and one had a confirmed nest tree. We observed owls roosting at territories during the diurnal and twilight hours, except at one territory, where we visually detected a family of owls (i.e., an adult pair with three juveniles) at night, but did not detect them on follow-up surveys. Of the 13 historical territories we surveyed, only 3 (23%) remained occupied. Out of the eight occupied territories, our third survey method detected four, our second survey method detected three, and our first survey method detected one.

In our initial set of logistic regression models comparing present conditions at currently occupied and vacant territories, the top-ranked model incorporated the basal area of deciduous trees as the sole predictor (Table 1). All other models surpassing the null model contained uninformative parameters; specifically, the other single-predictor models performed worse than the null model, had 85% confidence intervals overlapping with zero, and were >2 ΔAICc from the top model. Spotted owls were currently more likely to occupy territories with a greater basal area of deciduous trees (β = 2.83; 85% confidence interval, 1.30–5.28; Fig. 2). In our second set of logistic regression models comparing historical and present conditions at currently unoccupied territories, the highest ranked model included drought-related tree mortality (Table 1). No other predictors in the remaining set came within 2 AICc units of the highest ranked model, and none had an AIC weight exceeding 0.01. Based on this model, currently vacant territories had greater levels of drought-related tree mortality after the period of detection of the last owls (β = −3.70; 85% confidence interval, −7.00 to −1.68; Fig. 3).

DISCUSSION—Our study suggests that California spotted owl–occupied territories are rare across Southern California's Los Padres and Angeles national forests. Older forests that constitute spotted owl nesting habitat are naturally sparse in

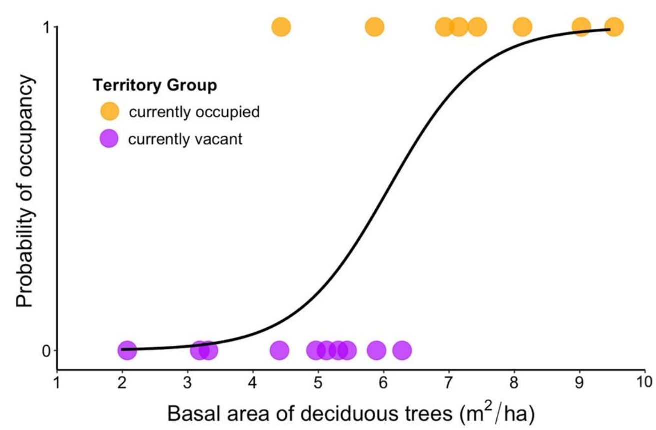

FIG. 2—Relationship between the basal area of deciduous trees and probability of spotted owl territory occupancy in Southern California, USA. The plot shows the probabilities of occupancy for both currently occupied (n = 8) and vacant (n = 10) territories. We z-transformed predictors for statistical analyses, but plotted them at their original values. To aid the visualization of overlapping points, we used the jitter function in R.

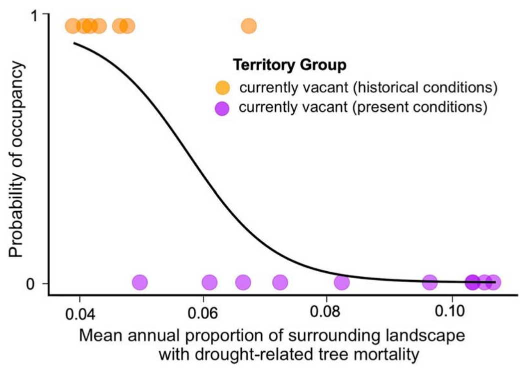

Fig. 3—Relationship between annual drought-related tree mortality estimates and probability of spotted owl territory occupancy in vacant territories during present and historical conditions in Southern California, USA. The plot shows the probabilities of occupancy based on tree mortality estimates for both present and historical conditions. We z-transformed predictors for statistical analyses but plotted them at their original values. To aid the visualization of overlapping points, we used the jitter function in R.

many parts of the Los Padres and Angeles national forests such that owl densities may be naturally low in these areas. However, many historically occupied territories are now vacant, suggesting that low owl densities may be linked to regional population declines (Tempel et al., 2022). We recognize that our predominantly two-visit approach, as opposed to the conventional range of three to six visits, along with the potential for intermittent or ongoing owl occupation since the last documented occupancy, may have led to undetected owls in presumed vacant territories. Although our single survey season prevents us from making quantitative inferences on population change in our study area, our results imply that, at the least, spotted owls are currently rare in our study area, even in areas classified as "good habitat" and are geographically isolated (Figs. S1 and S3). Thus, considering the large declines observed in other parts of this region (Tempel et al., 2022), spotted owls are becoming rare or experiencing declines throughout Southern California, with apparently no demographically stable populations.

The rarity of spotted owls in our study area may be, at least partially, the result of drought-related tree mortality because we detected greater amounts of tree mortality at vacant territories after the loss of territorial owls than the period of historical occupancy. California has undergone progressive drought since 2012, described as a 1 in a 1,200-yr event (Griffin and Anchukaitis, 2014; Asner et al., 2016). In the central and southern Sierra Nevadas, where the study of drought-related tree mortality has been extensive during this period, tree mortality is substantially higher in climatically drier areas (i.e., lower elevations and latitudes), in areas with shallow soils, on shallower slopes, and at greater distances from water (Paz-Kagan et al., 2017; Fettig et al., 2019; Restaino et al., 2019). Severe drought anomalies have also become more prevalent in coastal and Southern California (Williams et al., 2015); therefore, owl territories located in lower elevation forests may be particularly vulnerable to severe drought stress. In addition, anthropogenic water extraction activities may worsen these effects by depriving forests of water, leading to higher tree mortality, stream desiccation, and changes to the prey base (Beck and Gould, 1992). However, the sample size of territories was small and we acknowledge that we did not detect a difference in drought-related tree mortality between currently vacant territories and occupied territories. Broader scale population declines documented in the San Bernardino Mountains do not appear to be predominantly from drought-related tree mortality (Tempel et al., 2022), suggesting that any drought effects that we documented in our study were local.

We also found a positive relationship between territory occupancy and the presence of deciduous trees when comparing currently vacant and occupied territories, where the loss of large oaks could reduce the availability of suitable nest and roost sites and increase thermal exposure. Compared with other parts of the California spotted owl's range, the mountain ranges of Southern California are relatively hot and dry, with sparsely distributed forested areas at lower elevations limited to canyon bottoms and drainages—and associated forest–climate interactions could be contributing to population declines. In these warm, low-elevation areas, spotted owls tend to colonize territories with greater densities of large trees, potentially because they provide cooler microclimates (Tempel et al., 2022). Moreover, extreme heat events consistently result in ambient temperatures exceeding the upper critical limit of spotted owls in low-elevation territories, even when canopy cover is high (McGinn et al., 2023*a*), and in turn, could lead to energy conservation strategies that compromise foraging or breeding success (McGinn et al., 2023*b*). Thus, climate warming may render some territories, particularly low-elevation territories lacking sufficient large trees, thermally unsuitable for spotted owls and contribute both to the rarity of spotted owls that we observed here and to broader, regional scale declines across Southern California. Thermally unsuitable habitats may also become more prevalent because of the loss of large oak trees from disease (e.g., sudden oak death syndrome) and novel invasive pests (e.g., goldspotted oak borer [*Agrilus auroguttatus*]). The goldspotted oak borer, a new and potentially devastating pest of oak (*Quercus* spp.), has resulted in notable oak declines in the surrounding forests of Southern California (Coleman and Seybold, 2008), thereby threatening potentially suitable habitat for spotted owls. However, as is the case with tests of drought-related tree mortality, the sample size of territories was sparse and we acknowledge that larger sample sizes are important to identify broader scale patterns of territory loss with vegetation change.

Spotted owl habitat has also been lost in some areas in the Los Padres and Angeles national forests from recent severe wildfires (Higuera and Abatzoglou, 2021; Fig. S4). There is evidence that suggests spotted owls typically avoid foraging beyond 100 m into large patches of severely burned forests (Jones et al., 2020) and that territory occupancy rates decrease with greater amounts of severe wildfire (Lee et al., 2013; Jones et al., 2016; Kramer et al., 2021). In the San

Bernardino and San Jacinto mountains, Tempel et al. (2022) showed that owl territory extinction rates increased with the amount of high-severity wildfire in 10 yr and that colonization rates decreased to nearly zero when ≥40% of a territory experienced high-severity wildfire burn within 10 yr. However, the rarity of occupied territories in this study did not appear to be predominately the result of severe wildfire, given that we did not detect a difference in the amount of severe wildfire between currently occupied and vacant territories, nor differences at vacant territories during the period of historical occupancy and after losing territorial owls, although we acknowledge the power to detect this impact is likely limited because of our small sample sizes. Broader scale population declines documented in Southern California do not appear to be predominantly from severe wildfires, given that Tempel et al. (2022) found that high-severity wildfire only accounted for 10% of the observed decline in spotted owl occupancy in the San Bernardino Mountains from 1991 to 2019. Certainly, severe wildfires resulting from climate change and fire suppression pose a significant threat to spotted owls in Southern California, but do not appear to be the primary cause of the rarity and decline in spotted owls that we and others have documented in Southern California. At burned sites, postfire salvage logging can decrease the odds of occupancy of the site by spotted owls (Lee and Bond, 2015; Jones and Peery, 2019), potentially further compounding the challenges that these birds face in recovering after severe wildfires.

Several other unmeasured environmental factors could contribute to the rarity of spotted owls in Southern California, including human recreation, air pollution (LaHaye and Gutiérrez, 2005), and anticoagulant rodenticide exposure (Hofstadter et al., 2021). Among these factors, anticoagulant rodenticide exposure is a potentially significant threat, given high exposure rates near the wildland–urban interface in other parts of the spotted owl's range (Gabriel et al., 2018; Wiens et al., 2019; Hofstadter et al., 2021). Indeed, a combination of these stressors has the potential to cause cumulative effects on spotted owls that ultimately contribute to low densities and declining territory occupancy in the region. Ultimately, further research is necessary to conclusively determine the causes of these declines in Southern California's spotted owl population.

With extreme heat events, wildfires, and drought becoming more severe and frequent, and with the growing human population, forested habitats in Southern California are likely to continue to decline and become more fragmented. In principle, increasing connectivity could help prevent the extirpation of small isolated populations (Conlisk et al., 2021), but rescue effects in Southern California are unlikely given the lack of healthy source populations and the distances between mountain ranges that generally exceed dispersal distance. Thus, we suggest that the most effective strategy to conserve spotted owls in Southern California may be to maintain and promote tall, closed-canopy forests, especially from severe wildfires at high elevations and particularly in the San Bernardino Mountains, which harbor the largest remaining spotted owl populations. These high-elevation forests are key because they 1) provide accessible microclimates for owls to roost and nest during extreme heat events; and 2) support important, resource-rich prey items for spotted owls, including dusky-footed woodrats. Considering the recent proposal to list the Coastal-Southern California populations as endangered under the Endangered Species Act, these findings offer insights into the present condition of spotted owls in Southern California.

We thank the United States Forest Service Region 5, the California Department of Fish and Wildlife, the United States Fish and Wildlife Service, and the Wisconsin Agricultural Experiment Station for funding. We also thank T. Lavictoire, L. Bulbenko, M. Ondo, E. Gordon, and M. Holden for assistance in the field and S. Sawyer, P. Lieske, A. Berkley, and L. Welch for assistance with accessing field survey locations. We thank K. Keiser for providing historical spotted owl detection locations. We also thank K. Gallardo for assistance in writing the Resumen.

Literature Cited

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x.

Asner, G. P., P. G. Brodrick, C. B. Anderson, N. Vaughn, D. E. Knapp, and R. E. Martin. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proceedings of the National Academy of Sciences of the United States of America 113:E249–E255. https://doi.org/10.1073/pnas.1523397113.

Beck, T. W., and G. I Gould, Jr. 1992. Chapter 13: background and the current management situation for the California spotted owl in The California spotted owl: a technical assessment of its current status. Pacific Southwest Research Station, United States Department of Agriculture Forest Service. Genreal Technical Report PSW-GTR-133. https://doi.org/10.2737/PSW-GTR-133.

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2019. Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. Journal of Applied Ecology 56:470–480. https://doi.org/10.1111/1365-2664.13265.

Burnham, K. A., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York.

Cocking, M. I., J. M. Varner, and R. L. Sherriff. 2012. California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. Forest Ecology and Management 270:25–34. https://doi.org/10.1016/j.foreco.2011.12.039.

Coleman, T. W., and S. J. Seybold. 2008. Previously unrecorded damage to oak, *Quercus* spp., in southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse. Pan-Pacific Entomologist 84:288–300. https://doi.org/10.3956/2008-18.1.

Collins, B. M., D. L. Fry, J. M. Lydersen, R. Everett, and S. L. Stephens. 2017. Impacts of different land management histories on forest change. Ecological Applications 27:2475–2486.

Conlisk, E., E. Haeuser, A. Flint, R. L. Lewison, and M. K. Jennings. 2021. Pairing functional connectivity with population dynamics to prioritize corridors for Southern California spotted owls. Diversity and Distributions 27:844–856. https://doi.org/10.1111/ddi.13235.

Conner, M. M., J. J. Keane, C. V. Gallagher, G. Jehle, T. E. Munton, P. A. Shaklee, and R. A. Gerrard. 2013. Realized population change for long-term monitoring: California spotted owl case study. Journal of Wildlife Management 77:1149–1458.

Conner, M. M., J. J. Keane, C. V. Gallagher, T. E. Munton, and P. A. Shaklee. 2016. Comparing estimates of population change from occupancy and mark-recapture models for a territorial species. Ecosphere 7:e01538. https://doi.org/10.1002/ecs2.1538.

Diller, L. V., K. A. Hamm, D. A. Early, D. W. Lamphear, K. M. Dugger, C. B. Yackulic, C. J. Schwarz, P. C. Carlson, and T. L. McDonald. 2016. Demographic response of northern spotted owls to barred owl removal: barred owl removal experiment. Journal of Wildlife Management 80:691–707. https://doi.org/10.1002/jwmg.1046.

Eidenshink, J., B. Schwind, K. Brewer, Z. -L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–21. https://doi.org/10.4996/fireecology.0301003.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164–178. https://doi.org/10.1016/j.foreco.2018.09.006.

Forsman, E. D. 1983. Methods and materials, for locating and studying spotted owls. United States Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-GTR-12.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. Ornithological Monographs 54:1–54. https://doi.org/10.2307/40166799.

Gabriel, M. W., L. V. Diller, J. P. Dumbacher, G. M. Wengert, J. M. Higley, R. H. Poppenga, and S. Mendia. 2018. Exposure to rodenticides in northern spotted and barred owls on remote forest lands in northwestern California: evidence of food web contamination. Avian Conservation and Ecology 13:2. https://doi.org/10.5751/ACE-01134-130102.

Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? Geophysical Research Letters 41:9017–9023. https://doi.org/10.1002/2014GL062433.

Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*): life histories for the 21st century. In The birds of North America, no. 179: life histories for the 21st century (A. Poole and F. Gill, editors). The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D.C.

Gutiérrez, R. J., P. N. Manley, and P. A. Stine. 2017. The California spotted owl: current state of knowledge. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-254. https://doi.org/10.2737/PSW-GTR-254.

Gutiérrez, R. J., and J. Pritchard. 1990. Distribution, density, and age structure of spotted owls on two Southern California habitat islands. Condor 92:491–495. https://doi.org/10.2307/1368246.

Higuera, P. E., and J. T. Abatzoglou. 2021. Record-setting climate enabled the extraordinary 2020 fire season in the western United States. Global Change Biology 27:1–2. https://doi.org/10.1111/gcb.15388.

Hobart, B. K., G. M. Jones, K. N. Roberts, B. P. Dotters, S. A. Whitmore, W. J. Berigan, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2019. Trophic interactions mediate the response of predator populations to habitat change. Biological Conservation 238:108217. https://doi.org/10.1016/j.biocon.2019.108217.

Hofstadter, D. F., N. F. Krysiak, M. W. Gabriel, C. M. Wood, G. M. Wengert, B. P. Dotters, K. N. Roberts, E. D. Fountain, K. G. Kelly, J. J. Keane, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2021. High rates of anticoagulant rodenticide exposure in California barred owls are associated with the wildland–urban interface. Ornithological Applications 123:1–13. https://doi.org/10.1093/ornithapp/duab036.

Jones, G. M., R. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300–306. https://doi.org/10.1002/fee.1298.

Jones, G., J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2018. Declining old-forest species as a legacy of large trees lost. Diversity and Distributions 24:341–351. https://doi.org/10.1111/ddi.12682.

Jones, G. M., H. A. Kramer, W. J. Berigan, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2021. Megafire causes persistent loss of an old-forest species. Animal Conservation 24:925–936. https://doi.org/10.1111/acv.12697.

Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, T. Erker, F. A. Atuo, N. F. Pietrunti, R. Kelsey, R. J. Gutiérrez, and M. Z. Peery. 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecology 35:1199–1213. https://doi.org/10.1007/s10980-020-01010-y.

Jones, G. M., and M. Z. Peery. 2019. Phantom interactions: use odds ratios or risk misinterpreting occupancy models. Condor 121:1–7. https://doi.org/10.1093/condor/duy007.

Koltunov, A., C. M. Ramirez, S. L. Ustin, M. Slaton, and E. Haunreiter. 2020. eDaRT: the Ecosystem Disturbance and Recovery Tracker system for monitoring landscape disturbances and their cumulative effects. Remote Sensing of Environment 238:111482. https://doi.org/10.1016/j.rse.2019.111482.

Kramer, A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery. 2021. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management 479:118576. https://doi.org/10.1016/j.foreco.2020.118576.

LaHaye, W. S., and R. J. Gutiérrez. 2005. The spotted owl in Southern California: ecology and special concerns for maintaining a forest-dwelling species in a human-dominated desert landscape. United States Department of Agriculture Forest Service, General Technical Report 11.

LaHaye, W. S., R. J. Gutiérrez, and H. R. Akcakaya. 1994. Spotted owl metapopulation dynamics in Southern California. Journal of Animal Ecology 63:775–785. https://doi.org/10.2307/5255.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1992. Demography of an insular population of spotted owls (*Strix occidentalis occidentalis*). Pages 803–814 in Wildlife 2001: populations (D. R. McCullough and R. H. Barrett, editors). Elsevier, London, United Kingdom.

LaHaye, W. S., R. J. Gutiérrez, and J. R. Dunk. 2001. Natal dispersal of the spotted owl in Southern California: dispersal profile of an insular population. Condor 103:691–700.

LaHaye, W. S., G. S. Zimmerman, and R. J. Gutiérrez. 2004. Temporal variation in the vital rates of an insular population of spotted owls (*Strix occidentalis occidentalis*): contrasting effects of weather. Auk 121:1056–1069.

Lee, D. E., and M. L. Bond. 2015. Previous year's reproductive state affects spotted owl site occupancy and reproduction responses to natural and anthropogenic disturbances. Condor 117:307–319. https://doi.org/10.1650/CONDOR-14-197.1.

Lee, D. E., M. L. Bond, M. I. Borchert, and R. Tanner. 2013. Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto mountains of Southern California: fire and spotted owl dynamics. Journal of Wildlife Management 77:1327–1341. https://doi.org/10.1002/jwmg.581.

McGinn, K. A., M. Z. Peery, C. J. Zulla, W. J. Berigan, Z. A. Wilkinson, J. M. Barry, J. J. Keane, and B. Zuckerberg. 2023a. A climate-vulnerable species uses cooler forest microclimates during heat waves. Biological Conservation 283:110132. https://doi.org/10.1016/j.biocon.2023.110132.

McGinn, K. A., B. Zuckerberg, J. N. Pauli, C. J. Zulla, W. J. Berigan, Z. A. Wilkinson, J. M. Barry, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2023b. Older forests function as energetic and demographic refugia for a climate-sensitive species. Oecologia 202:831–844. https://doi.org/10.1007/s00442-023-05442-6.

Noon, B. R., and K. S. McKelvey. 1992. Stability properties of the spotted owl metapopulation in Southern California. Pages 187–206 in The California spotted owl: a technical assessment of its current status. Pacific Southwest Research Station, United States Department of Agriculture Forest Service, General Technical Report PSW-GTR-133.

Paz-Kagan, T., P. G. Brodrick, N. R. Vaughn, A. J. Das, N. L. Stephenson, K. R. Nydick, and G. P. Asner. 2017. What mediates tree mortality during drought in the southern Sierra Nevada? Ecological Applications 27:2443–2457.

Restaino, C., D. J. N. Young, B. Estes, S. Gross, A. Wuenschel, M. Meyer, and H. Safford. 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. Ecological Applications 29:e01902. https://doi.org/10.1002/eap.1902.

Smith, R. B., M. Z. Peery, R. J. Gutiérrez, and W. S. LaHaye. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. Wilson Bulletin 111:22–29.

Tempel, D. J., H. A. Kramer, G. M. Jones, R. J. Gutiérrez, S. C. Sawyer, A. Koltunov, M. Slaton, R. Tanner, B. K. Hobart, and M. Z. Peery. 2022. Population decline in California spotted owls near their southern range boundary. Journal of Wildlife Management 86:e22168. https://doi.org/10.1002/jwmg.22168.

Tempel, D. J., M. Z. Peery, and R. J. Gutiérrez. 2014a. Using integrated population models to improve conservation monitoring: California spotted owls as a case study. Ecological Modelling 289:86–95. https://doi.org/10.1016/j.ecolmodel.2014.07.005.

Tempel, D. J., R. J. Gutiérrez, S. A. Whitmore, M. J. Reetz, R. E. Stoelting, W. J. Berigan, M. E. Seamans, and M. Z. Peery. 2014b. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. Ecological Applications 24:2089–2106.

United States Fish and Wildlife Service. 1990. 50 CFR part 17 endangered and threatened wildlife and plants; determination of threatened status for the northern spotted owl; final rule. Federal Register 55:26114–26194.

United States Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants; Final rule to list the Mexican spotted owl as threatened. Federal Register 58:14248–14271.

United States Fish and Wildlife Service. 2023. Endangered and threatened wildlife and plants; California spotted owl; endangered status for the coastal-Southern California distinct population segment and threatened status with Section 4(d) Rule for the Sierra Nevada Distinct Population Segment. United States Department of Agriculture, Docket ID FWS-R8-ES-2022-0166.

Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck. 1992. Assessment of the current status of the California spotted owl, with recommendations for management. Pages 3–26 in The California spotted owl: a technical assessment of its current status. Pacific Southwest Research Station, United States Department of Agriculture Forest Service, General Technical Report PSW-GTR-133.

Wiens, J. D., K. E. Dilione, C. A. Eagles-Smith, G. Herring, D. B. Lesmeister, M. W. Gabriel, G. M. Wengert, and D. C. Simon. 2019. Anticoagulant rodenticides in *Strix* owls indicate widespread exposure in west coast forests. Biological Conservation 238:108238. https://doi.org/10.1016/j.biocon.2019.108238.

Wiens, J. D., K. M. Dugger, J. M. Higley, D. B. Lesmeister, A. B. Franklin, K. A. Hamm, G. C. White, K. E. Dilione, D. C. Simon, R. R. Bown, P. C. Carlson, C. B. Yackulic, J. D. Nichols, J. E. Hines, R. J. Davis, D. W. Lamphear, C. McCafferty, T. L. McDonald, and S. G. Sovern. 2021. Invader removal triggers competitive release in a threatened avian predator. Proceedings of the National Academy of Sciences of the United States of America 118:e2102859118. https://doi.org/10.1073/pnas.2102859118.

Williams, A. P., R. Seager, J. T. Abatzoglou, B. I. Cook, J. E. Smerdon, and E. R. Cook. 2015. Contribution of anthropogenic warming to California drought during 2012–2014. Geophysical Research Letters 42:6819–6828. https://doi.org/10.1002/2015GL064924.

Zimmerman, G. S., W. S. LaHaye, and R. J. Gutiérrez. 2001. Breeding-season home ranges of spotted owls in the San Bernardino Mountains, California. Western Birds 32:83–87.

Submitted 13 November 2023. Accepted 13 February 2025.
Associate Editor was Medhavi Ambardar.