California Spotted Owl Occupancy On Mixed-Ownership Lands In the Sierra Nevada of California, 2012 Through 2016

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CALIFORNIA SPOTTED OWL OCCUPANCY ON MIXED-OWNERSHIP LANDS IN THE SIERRA NEVADA OF CALIFORNIA, 2012 THROUGH 2016

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ABSTRACT—Since the 1970s, California Spotted Owls (*Strix occidentalis occidentalis* [CSO]) have been documented on private forest lands currently owned by Sierra Pacific Industries (SPI) in the Sierra Nevada of California. In 2012, SPI began an occupancy study on a portion of the CSO population known to occur on or near its managed forests in 5 watershed study areas averaging 110 km^2 each. These watersheds occur from the southern end of the Cascade Range to just north of Yosemite National Park. We concluded that 57 historical CSO sites existed in these areas at the beginning of the study. During 2012 through 2016, the survey effort increased the total number of known CSO sites in the study areas to 65. During the same period, the yearly occupancy of the CSO sites within the study areas ranged from 70 to 86%, with 98% of the sites occupied during at least 1 y. Crude densities during the study period were calculated to be 0.117 CSO-occupied sites km^{-2}. Compared to other studies in the Sierra Nevada, the CSO populations on our 5-yr study areas showed relatively high occupancy rates and a wide range of crude densities.

Key words: California Spotted Owl, detection probability, occupancy, Sierra Nevada, *Strix occidentalis occidentalis*,

The Spotted Owl (*Strix occidentalis*) occupies territories across forested landscapes and shows a preference for stands of larger and denser timber for nesting sites (Gutiérrez and others 1992; Franklin and others 2000). Through the early 1990s, most of the private lands in the Sierra Nevada, California, had not been inventoried for California Spotted Owls (*Strix occidentalis occidentalis*, CSOs); thus, little information was available on CSO presence, occurrence, or abundance on these lands (Verner and others 1992). Some researchers suggested that lands managed for timber production might not provide habitat suitable for occupancy by the CSO subspecies (Bias and Gutiérrez 1992) and that private lands were not used in proportion to their availability for CSO foraging (Williams and others 2014). Additionally, in a 2004 petition to list the CSO as threatened or endangered under the federal Endangered Species Act, timber harvest on private lands was identified as an action that "threatens to further degrade and destroy spotted owl habitat, resulting in continued declines in numbers of spotted owls" (US

Fish and Wildlife Service 2006). A more recent petition seeking listing under the federal Endangered Species Act stated that the CSO "is being heavily impacted by logging on private lands" (Sierra Forest Legacy and Defenders of Wildlife 2015).

Three of 4 ongoing studies of the CSO on public lands, or where public lands were the majority of the study area, have reported declines in population size. Between 1990 and 2011, Conner and others (2013) reported declines in population size of 11 and 21% for the Lassen and Sierra National Forest study areas, respectively, and a 22% increase for the Sequoia Kings Canyon (National Park) study area. Tempel and Gutiérrez (2014) reported a 30% decline in occupancy and a decline of approximately 29% in population size at the Eldorado Study Area (EDSA) between 1993 and 2010.

Given the long history of widespread timber harvest in the Sierra Nevada (Verner and others 1992) and the rather even distribution and spacing of reported responses of CSOs across this mountain range (Verner and others 1992; USFWS 2003; CNDDB 2015), it appears that the CSO is presently occupying landscapes in which there have been recent forest-management activities.

Over the last several decades, intermittent surveys for CSOs were conducted on lands in private ownership to establish protection areas in advance of timber operations. During the 1990s, many CSO sites were identified by only a single nighttime response. A thorough CSO occupancy study on private lands had not been conducted. In 2012, Sierra Pacific Industries (SPI) began a comprehensive annual occupancy study on a portion of the CSO population known to occur on and adjacent to their Sierra Nevada forest lands to determine if CSOs currently and consistently occupy these landscapes where there have been ongoing, intensive forest-management activities.

Methods

Study Areas

The study included 5 watershed study areas (WSAs) in the Sierra Nevada from the southern end of the Cascades to just north of Yosemite National Park: (from north to south) Fall River (FARI), Chalk Bluff (CHBL), Stumpy Meadows Study Area (SMSA), South Fork Cosumnes River (SFCR), and South Fork Mokelumne River (SFMR) (Fig. 1). These study areas were selected for their distribution across the Sierra Nevada within the elevation range of the CSO, their relatively high proportion of SPI ownership, and their history of CSO surveys. The SMSA area was particularly chosen because it also contained an area previously studied by Laymon (1988) and had documented extensive surveys efforts in 1991–1992 and 2003–2006 (SPI, unpubl. data). Proximity of the WSAs to other CSO study areas such as the Lassen study area (Keane and others 2010) and the EDSA (Peery and others 2013) allowed for comparisons of occupancy and density. The WSAs were approximately 16 to 46 km from each other, stretching over 158 km of the central Sierra Nevada. The study areas ranged between 664 and 2005 m in elevation. We characterized the habitat in the region as mainly Sierran mixed-conifer, with areas of conifer, hardwood, and chaparral (Allen 1988).

The 5 WSAs ranged from 85.7 to 137.1 km^2 in size ($\bar{x} = 109.7$ km^2, $s = 22.1$ km^2); all were near or in the study area size of 90 to 130 km^2 recommended by Franklin and others (1990) for accurate estimation of Spotted Owl densities. Each WSA comprised 3 or 4 contiguous planning watersheds (16 planning watersheds total) as designated by CalWater (Cal Fire 2004). In the CHBL WSA we removed 19.49 km^2 of forested residential subdivision and 16.13 km^2 of unforested mine tailings from the CSO study, as these areas were considered unusable by the CSO (Table 1). The remaining adjusted area of the combined CSO WSAs was 548.5 km^2. SPI ownership averaged 52.5% of the lands in these study areas (s = 22.4%; range = 26.8 to 68.8%), with other privately held and US Forest Service lands making up the remainder (Table 1).

Prior to 1999, various owners repeatedly harvested the lands currently owned by SPI, primarily using selection methods that removed large individual tress in repeated harvests during the past 50 to 100 y. Since 1999, SPI has been implementing an even-aged management strategy (clear cutting and regeneration of forest stands). By 2016, approximately 26 to 28% of the SPI land base within the WSAs had been converted to forest stands ranging from 0 to 17 y old (Ed Murphy, Sierra Pacific Industries, Anderson, CA, pers. comm.). Since 1999, SPI has also consistently provided a minimum of 7.28 ha of protection around all recorded CSO activity

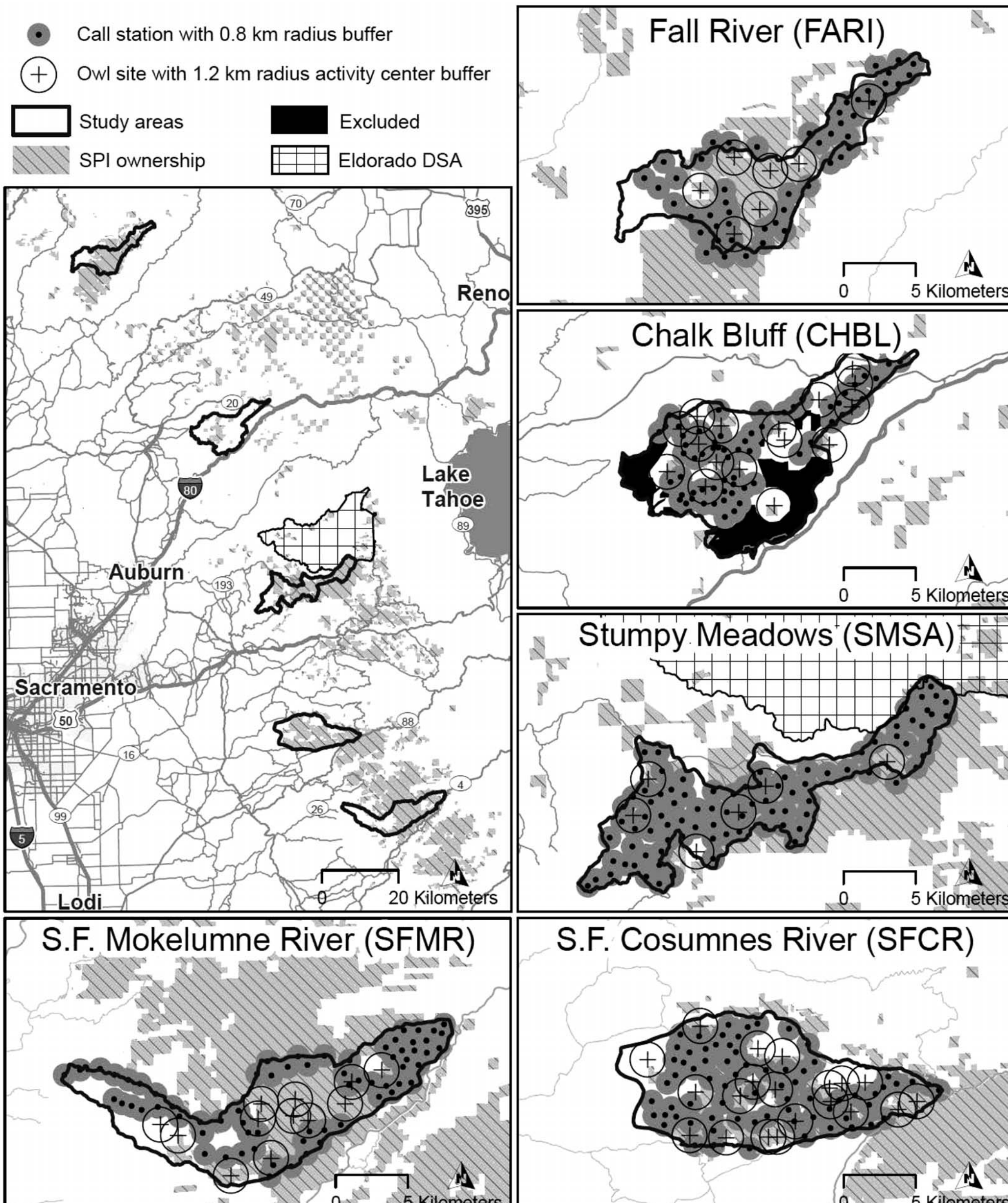

FIGURE 1. SPI's watershed study areas for the California Spotted Owl (CSO) in the Sierra Nevada, California, 2012–2016.

centers by not harvesting units where owl sites occur. Also, SPI's implementation of the California Forest Practice Rules with their clear-cut adjacency limits has resulted in larger areas of unharvested forest around CSO activity centers. Much of the USFS land within the study area also had been selectively harvested to varying degrees in the past, but had not been harvested to a significant degree in the last 20 y (Verner and others 1992; Sierra Nevada Ecosystem Project 1996; USDA Forest Service 2003, 2015a). Only limited harvesting has occurred recently on the other private lands in the study areas (Long 2012). Prior to 2014, only minor fires (<10 km^2)

TABLE 1. SPI's California Spotted Owl watershed study area sizes and ownership percentages. Sierra Nevada, California.

Study area	Total area (km^2)	Area considered unusable habitat* (km^2)	Adjusted habitat area (km^2)	SPI ownership		Federal ownership		State ownership		Other private ownership	
				(km^2)	(%)	(km^2)	(%)	(km^2)	(%)	(km^2)	(%)
FARI	88.57	0	88.57	58.72	66.3	22.84	25.8	0	0.0	7.01	7.9
CHBL	121.28	35.62	85.66	22.97	26.8	44.46	51.9	0	0.0	18.23	21.3
SMSA	115.37	0	115.37	79.42	68.8	28.29	24.5	4.49	3.9	3.17	2.7
SFCR	137.05	0	137.05	85.81	62.6	8.45	6.2	0	0.0	42.78	31.2
SFMR	121.84	0	121.84	41.16	33.8	61.02	50.1	0	0.0	19.66	16.1
Total and %	584.11	35.62	548.49	288.08	52.5	165.06	30.1	4.49	0.8	90.85	16.6

* Residential and mine tailings, including 4.05 km^2 of USFS lands, 0.08 km^2 of SPI lands, and 31.49 km^2 other private ownership by other parties.

occurred in the study areas (CDF-FRAP 2014). In 2014, the King Fire burned 38.6 km^2 (33.5%) of the SMSA area, primarily at high severity (USDA Forest Service 2014), causing 1 CSO site to become unoccupied during this study and prior to any salvage logging of the burned forest. Additionally, during the 2016 season a new site was found near the fire's edge in the SMSA.

Surveys

For purposes of this study we defined a CSO site as the combined general area of the reported yearly activity centers for CSO locations recorded in the California Natural Diversity Database (CNDDB 2015) or the SPI database, or an area where a CSO responded multiple times to broadcast calls in a given year or over multiple years. Prior to initiation of fieldwork, we searched then-current databases (for example, CNDDB 2015) for all recorded CSO sites within the study areas. Documentation of historical records in publicly available data was often incomplete, and we found that in the past CSO locations were sometimes designated from a single owl-response event. A total of 63 historical locations had been included in the various databases for the WSAs. After our detailed review, and based on our fieldwork prior to this study, we concluded that 57 CSO locations met our criteria for valid CSO sites by demonstrating a history of territorial occupancy at the initiation of our occupancy study in 2012. Forty-five (79%) of these sites had been recorded prior to 1996, and 50 sites (89%) prior to 2000. The true numbers of occupied sites at various intervals in the past are unknown, because past surveys were not comprehensive.

We attempted to locate CSOs in each WSA annually using several approaches. All of these methods were employed from 15 March through 15 August of each year, 2013–2016. WSA-wide surveys were not conducted in 2012, only CSO site surveys and activity-center searches (further described below). First, based on half the average nearest-neighbor distance for the 60 CSO sites known in 2013, we established 1.21-km-radius circles centered on the last known activity center of each owl site. We then used diurnal (daylight hours or within 1 h of sunrise-sunset) walk-ins to search for current owl-activity centers (nest or roost site) within these circles; Spotted Owls are typically found near their core-use areas during the day (USFWS 1992, 2012; Franklin and others 1996; Peery and others 2013). If occupancy and social status were not determined during the 1st walk-in survey, we expanded the effort to cover more of the 1.21-km circle with diurnal walk-in searches and with nighttime acoustical surveys in the known circles, as necessary.

Outside of the activity-center circles, we conducted nighttime acoustical surveys from 283 permanent call stations that averaged approximately 1 km apart along the well-distributed road system (Fig. 1). These stations were called in all subsequent years. We first established call stations in and around the larger and denser forest stands and then distributed them to the other habitats within the WSAs. Nighttime surveys typically started 1 h prior to sunset and continued until midnight, playing recorded calls from each station for a maximum of 10 min or until a CSO response was elicited.

We conducted up to 3 nighttime surveys at each established call station and within each known circle (where necessary). At least 1 visit occurred before 1 June and at least 1 after 1 June each year if occupancy had not been established before 1 June. At call stations, visits with no CSO responses were at least 13 d apart. Within 72 h of detecting an owl from a call station, we followed with a diurnal walk-in survey. If owls detected from call stations were not found during diurnal follow-up visits, we resumed surveying from the call stations until the 3-survey protocol was complete or the owls were found. When a new site was located, activity-center circles were designated for use in succeeding years where activity-center searches and nighttime surveys would occur. Established calling stations inside these new circles were dropped from future surveys.

To estimate the percent of the study areas covered by surveys, we totaled the area within the 1.21-km radius circles around all known CSO activity centers (incorporating the assumption that known occupancy of this area was equivalent to being fully surveyed), and the area of 0.8-km-radius circles around each of the established call stations, assuming that CSOs could hear our played calls and we could hear their response for that distance (USFWS 1992; Tempel and Gutiérrez 2013). As depicted in Figure 1, application of such circles resulted in scattered "slivers" of landscape that, under these assumptions, were unsurveyed. By area, these slivers totaled 17% of the overall study area. However, for several reasons described in the Results section, we doubt that we missed an equivalent number of CSO sites.

Social Status and Occupancy

Within 72 h of the initial detection of a CSO during the nighttime point surveys or during the activity-center search of the known sites, we attempted to determine the territorial occupancy and social status of owls at the site (Forsman 1983; USFWS 1992, 2012; Franklin and others 1996). We used acoustical surveys and live lures (mice) in the vicinity of CSO responses until occupancy, social, and reproductive status were determined (Forsman 1983; Franklin and others 1996). The combination of acoustic and live-lure techniques has been shown to be 94% effective for determining the status of a Spotted Owl site within 3 survey visits (Reid and others 1999). Each year, we assigned a site to 1 of 4 categories of occupancy: unoccupied, resident single, pair, or reproductive pair. CSO sites were considered to be unoccupied for the year if no CSO responded during the survey efforts (absent) or where only a single nighttime response was elicited during survey efforts (non-resident single). Where CSOs were found, social and reproductive status were determined by observing the owls and offering them live mice. Various behaviors indicated that the owls were resident singles (at least 2 detections of an unmated single owl), pairs, or reproductive pairs. Sites where CSOs exhibited these behaviors or where multiple nighttime auditory responses occurred were classified as occupied. Thus, a site was considered territorially occupied when we observed nesting or roosting owls or when an owl was repeatedly heard calling from or near the known site location (Olson and others 2005). When possible, we identified the activity-center point for each occupied site each year based on the nest or day-roost location. Typically, adjacent sites were surveyed simultaneously by survey crews to verify that the sites were occupied by different owls. After 3 consecutive years of no responses at a known CSO site, we removed 1 site from activity-center walk-in surveys and from the occupancy-rate calculation for 2016, but continued to survey the area as part of the WSA-wide survey efforts. Additionally, starting in 2013, we marked a majority of the adult owls encountered with uniquely colored leg-bands to aid in individual identification.

We analyzed detection probability (P) across all sites for all 5 y per MacKenzie and others (2003) and Conway and Simon (2003). For each year, we also calculated annual detection probability for each of the 3 yearly survey events.

We began this study using a removal sampling design because if occupancy of a site was established in the 1st or 2nd survey of the year, no additional surveys were needed (MacKenzie and others 2006). In subsequent years, we added efforts to determine social and reproductive status and to capture and band the owls, thus resulting in 3 or more visits to occupied sites. Both nighttime survey efforts and the daytime activity-center searches were used to calculate the probability of detection and the estimated occupancy. Daytime activity searches have been shown to increase the likelihood of a determination of residency and thus occupancy (Farber and Kroll 2012; USFWS 2012).

We used the program PRESENCE (Hines 2006) to determine the estimated proportion of occupied sites versus unoccupied sites, and to calculate rates of naïve and estimated occupancy. Because all habitat types within the adjusted area were surveyed for CSOs (Fig. 1), we determined the crude densities by dividing the number of observed occupied sites by the adjusted area of the WSA. We used 3–y rolling average to smooth the yearly fluctuations in occupancy and crude densities, and to compare to other studies in the Sierra Nevada when their data was sufficient.

Habitat

We described habitat using the California Wildlife Habitat Relationships (WHR) classifications (Mayer and Laudenslayer 1988) as supplied in the F-Veg data set (CDF-FRAP 2015), which is based on satellite and aerial photo images. We believed these data to be the best available and complete habitat layer of the forested environment in California; however, some of the data had not been updated since 1995. Therefore, we used SPI's most recent proprietary on-the-ground inventory database (1 variable-radius prism plot every 1.62 ha) to refine the WHR typing on the lands owned by SPI. Forest-habitat characteristics such as tree species, diameters, heights, and canopy dimensions were recorded by foresters at the established grid of plots covering all SPI lands in the WSAs. After sampling, we stratified these plots into stands described from the average of contained plots and classified into WHR types. No ground-based sampling data were available from other private and federal ownerships, so we could not similarly refine the F-Veg determination of habitats on those lands. Thus, to quantify habitat on other ownerships we used the WHR habitat types reported in F-Veg. We acknowledge that this may result in error in quantifying habitat, but have no feasible means to solve this within the scope of the current study. We used the habitat types that occurred most often at the activity-center points to determine the primary habitats for the CSOs in the WSAs.

Landscape Factors

Using the available habitat layers, we determined the percentage of area of the combined WHR classifications (tree size and canopy closure) for each WSA. Streams within the WSAs were identified and measured. We defined streams per the California Forest Practice Rules as "...any well-defined channel with distinguishable bed and bank showing evidence of having contained flowing water as indicated by deposits of rock, sand, gravel or soil..." (Cal Fire 2016). We determined the average ratio of surface area to planimetric area (or "roughness", a measure of topographic relief) of each WSA for each cell of a 10-m digital elevation model (DEM) using methods described by Jenness (2004).

We determined "edge" by measuring the linear edge between combined stands of WHR 4M, 4D, 5M, 5D, and 6 against all other WHR classifications, and then calculated the density of edge within each WSA on a per-km^2 basis. These WHR types were the primary habitats surrounding activity-center points in the EDSA and the WSAs. We used linear regression to assess the potential influence of each of the above landscape factors on densities of occupied sites.

Results

Surveys

Each year we conducted multiple surveys at all known sites and at 283 other established call stations in the WSAs. Our 2 sampling methods surveyed 83.1% of the total adjusted area within the WSAs, regardless of apparent habitat quality (Fig. 1). We identified 8 new sites, 7 of which were discovered during nighttime surveys at the periphery in the 1.21-km-radius circles surrounding the historical sites being monitored. The yearly WSA-wide nighttime call-station surveys resulted in the discovery of only 1 new site. These newly discovered sites were possibly present but missed during previous surveys.

Invasive Barred Owls (*Strix varia*) are known to be affecting Spotted Owl detection and occupancy elsewhere in California (Gutiérrez and others 2007a; Keane 2014). No Barred Owl activity centers were located in the WSAs, but 2 Barred Owl activity centers were found immediately adjacent to the SMSA. In 2013, 2014, and 2015, these Barred Owls hampered determination of occupancy and social status of the 2 nearest CSO sites, but we eventually found that both CSO sites were occupied in these years.

TABLE 2. Social status of surveyed California Spotted Owl sites by SPI's watershed study area and year. Sierra Nevada, California.

Study Area	2012 (n = 58)					2013 (n = 60)					2014 (n = 62)					2015 (n = 64)					2016 (n = 64)				
	U	S	RS	P	RP	U	S	RS	P	RP	U	S	RS	P	RP	U	S	RS	P	RP	U	S	RS	P	RP
FARI	1	0	5	1	0	3	2	0	3	0	3	1	0	1	3	2	1	1	3	2	3	1	1	3	2
CHBL	3	0	10	2	0	4	0	1	9	2	3	0	2	4	8	5	0	0	6	6	3	0	1	12	0
SMSA	1	0	4	1	0	2	1	1	2	0	1	2	2	0	1	1	1	1	2	1	1	1	1	4	0
SFCR	0	0	4	13	2	0	0	3	15	1	1	0	2	8	9	0	1	1	10	8	0	0	0	17	3
SFMR	3	0	3	4	1	3	3	0	3	2	2	1	3	2	3	0	3	1	4	4	1	2	3	5	1
Total	8	0	26	21	3	12	6	5	32	5	10	4	9	15	24	8	6	4	25	21	8	4	6	41	6
Young fledged					6					7					26					27					6
% yearly total	13.8	0	44.8	36.2	5.1	20.0	10.0	8.3	53.3	8.3	16.1	6.5	14.5	24.2	38.7	12.5	9.4	6.3	39.1	32.8	12.5	6.3	9.4	64.1	7.8

Key: U = Unoccupied; S = Single (non-resident); RS = Resident Single; P = Pair; RP = Reproductive Pair; CHBL = Chalk Bluff; FARI = Fall River; SFCR = South Fork Cosumnes River; SFMR = South Fork Mokelumne River; SMSA = Stumpy Meadows.

Barred Owls were not detected during the 2016 survey efforts.

Though only 83% of the area of the WSAs was covered by surveys, it is unlikely that we missed any additional CSOs in the WSAs in the remaining 17% because all high-quality habitat stands were surveyed and only small parcels of land were not covered. Despite several years of surveys with multiple surveys per year, only 1 new CSO site was found outside of activity-center circles of the known CSO sites.

Social Status and Occupancy

We detected CSOs at each of the 65 sites at least once during the study period. The highest social-status determinations for the sites during the 5-y study period were the following: 1 unoccupied (represented by a non-resident single), 5 resident singles, 24 pairs, and 35 reproductive pairs. In 2012, we reported only the occupancy determinations; reproductive attempts or success were not determined at all sites. From 2013 through 2016, we determined both social and occupancy status at all sites. A total of 56 reproductive attempts were documented (Table 2), with 66 young produced. This resulted in a mean of 1.2 young produced per known nesting attempt or reproductive pair for 2013 through 2016. In 2013, 5 nests produced 7 young; in 2014, 24 nests produced 26 young; in 2015, 21 nests produced 27 young; in 2016, 6 nests produced 6 young. Social status differed significantly among individual WSAs in 2012 ($P = 0.007$, $df = 4$), 2013 ($P = 0.018$, $df = 4$), 2015 ($P = 0.001$, $df = 4$), and 2016 ($P = 0.007$, $df = 4$). The number of resident singles decreased and the number of pairs increased between 2012 and 2013 ($P = 0.015$, $df = 4$), but not during the last 3 y of the study. During 2013–2016, we banded 78 adult CSOs. No banded owls were found occupying more than 1 territory in a single year.

The probabilities of detection for each year ranged from 0.895 in 2013 (95% C.I. = 0.770 – 0.964) to 0.987 in 2015 (95% C.I. = 0.961 – 0.998) (Table 3). For the 1st, 2nd, and 3rd survey events of known CSO sites, the average numbers of surveys conducted over the 5 y were 61, 55, and 45 respectively, yielding average single-survey probability detections of 0.64, 0.65, and 0.61, respectively.

The yearly observed occupancy rates of sites in the combined study areas were 86% in 2012,

TABLE 3. Yearly probability of detection and California Spotted Owl site-occupancy rates of SPI's watershed study areas in the Sierra Nevada, California.

Parameters of Occupancy	2012	2013	2014	2015	2016	Average
Naïve occupancy	0.86	0.80	0.82	0.91	0.88	0.85
Probability of detection	0.92	0.90	0.93	0.99	0.98	0.93
Estimated -Program PRESENCE (95% confidence interval)	0.88 (0.75–0.95)	0.83 (0.69–0.92)	0.84 (0.71–0.92)	0.91 (0.81–0.96)	0.88 (0.77–0.94)	0.86
Observed	0.86	0.70	0.77	0.78	0.81	0.79
Number of occupied sites	50	42	48	50	52	48.4
EDSA (Observed)*	0.40	0.46	0.42			0.43
Number of occupied sites	19	22	20			20.3

* Peery and others (2013, 2014, 2015). Data were unavailable for empty cells.

70% in 2013, 77% in 2014, 78% in 2015, and 81% in 2016 (Table 3). The mean occupancy within individual WSAs ranged between 61 and 98% for the 5 y combined. Annual occupancy of individual WSAs ranged from 38% at FARI in 2013 to 100% at SFCR in 2012, 2013, and 2016. Of the 65 sites known or discovered during this study, 64 (98%) were occupied at least once during the 5 y.

Within individual WSAs, there was no significant difference in occupancy ($\alpha = 0.05$) or social status ($P > 0.05$; $\alpha = 0.05$, $df = 2$) between 2012, 2013, 2014, 2015, or 2016. Between WSAs, occupancy differed significantly only in 2013, with lower occupancy rates in FARI and SMSA ($P = 0.001$, $df = 4$).

Naïve, estimated, and observed occupancies were consistently above 72%, with the naïve and estimated occupancy always higher than the observed occupancy (Fig. 2). The 5-y averages for the naïve, estimated, and observed occupancies were 0.85, 0.87, and 0.79 respectively.

We also calculated crude density for the study period. The overall average density for the WSAs (all years) was 0.117 occupied sites km^{-2}. The densities from the individual study areas ranged from 0.029 to 0.198 occupied sites km^{-2} (Table 2). Over the three 3-y rolling average periods during the study (2012–2014, 2013–2015, 2014–2016) the average number of occupied sites and the related crude densities decreased slightly (Table 4) despite an increase in the number of sites monitored for occupancy.

All of the 45 CSO sites that were known prior to 1996 were occupied at least once during the 5-y study period (2012–2016). On a yearly basis, these sites were occupied as follows: 2012 (86%), 2013 (70%), 2014 (78%), 2015 (76%), and 2016 (78%).

Based on the most recent site locations in the combined study areas, 62.5% of activity centers at occupied sites occurred on SPI-owned lands, 29.7% on USFS lands, and 7.8% on other private lands. The percentage of CSO activity centers on SPI lands was higher than the percentage of SPI land ownership in the combined study areas (62.5% of occupied sites versus 49% of available land base), although the difference was not significant ($P > 0.05$, x^2 =3 1.09, $df = 4$). For the individual study areas, the percentage of occupied sites on SPI lands was greater than the SPI lands available within 4 of the 5 study areas ($\bar{x}$ difference = 13.3%; s = 14.0; range = –2.1 to 32.9%). The percentage of CSO activity centers on USFS lands was higher than the percentage of that ownership available on 3 of the 5 study areas ($\bar{x}$ difference = 0.7%; s = 15.6%; range = –25.1 to 18.8%). SPI lands had 0.135 CSO sites km^{-2}, USFS lands had 0.118 CSO sites km^{-2}, and other lands had 0.039 CSO sites km^{-2}. CSO densities were not significantly different between SPI and USFS lands ($P = 0.556$, $df = 4$). CSO densities on other lands were significantly lower than those on USFS and SPI lands ($P = 0.046$, $df = 4$; $P = 0.012$, $df = 4$, respectively).

Habitat

We assessed the amounts of available WHR habitat types at 3 scales: the point location of the most recent activity center; the 29-ha (304-m-radius) area surrounding the point; and the entire WSA. Across all 5 WSAs combined, all 3

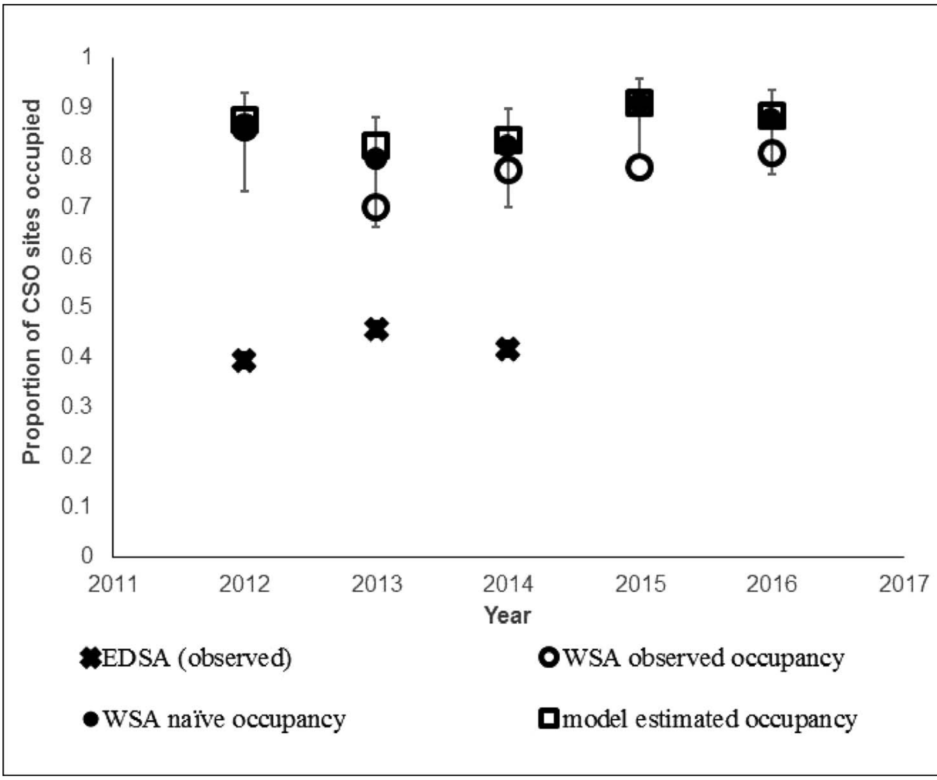

FIGURE 2. Proportion of the California Spotted Owl sites "occupied" (observed, naïve, and model estimate) in the combined 5 SPI watershed study areas and the Eldorado Density Study Area, Sierra Nevada, California.

scales were dominated by 5 WHR vegetation types: Sierran Mixed Conifer (53.2, 51.7, and 45.4% respectively), Montane Hardwood-Conifer (33.9, 29.7, and 20.4%), Ponderosa Pine (6.5, 11.1, and 15.5%), Douglas-fir (4.8, 3.0, and 5.8%), and Montane Hardwood (1.6, 1.8, and 5.2%).

WHR class 4D (trees 28–61 cm quadratic mean diameter and >60% canopy closure) was the predominant habitat class at all scales of analysis (Fig. 3). In combination, WHR classes 4M, 4D, and 5D accounted for 89% of the habitats at the CSO activity center points (5, 60, and 24%, respectively). Though no activity center points were documented in WHR 5M and 6, tree size and canopy cover in these classes are equal to or larger than classes found used by CSO, so we included these types in our defined primary habitat in analyses described below.

Landscape Factors

In an effort to explain the differences in the crude densities among our study areas (Table 4), we assessed linear relationships between the respective CSO crude densities in each of the WSAs and the amount of available primary habitat (WHR 4M, 4D, 5M, 5D, and 6 combined), length of stream courses, average weighted elevation, average surface area ratios, and the density of edge. Combined, 89% ($s = 36\%$) of the activity-center points and 82% ($s = 19\%$) of the 29-ha activity-center stand area consisted of primary habitats, but only 70% ($s = 8\%$) of the area of the combined WSAs consisted of this habitat (Fig. 3). However, we found only a weak correlation between the percentage of each WSA available as primary habitat and the crude densities of CSO sites at the WSA scale. We also found a weak negative correlation between CSO density and the density of edge. These relationships are detailed in Table 5. To an unknown degree, these analyses of forest habitat may be affected by the aforementioned unquantified error related to habitat typing. CSO densities were negatively correlated with density of

TABLE 4. Crude density of occupied California Spotted Owl sites per km^2 from SPI's Watershed Study Areas in the Sierra Nevada, California for three, 3-y rolling periods (2012–2014, 2013–2015, 2014–2016), and comparison to other studies.

Study area	Study area (km^2)	# of CSO occupied sites	Time period (y)	Average crude density of occupied sites km^{-2}	Citation
Combined WSAs	548.5	64	2012–2016	0.117	This study
Combined WSAs	548.5	60	2012–2014	0.109	This study
FARI	88.6	8	2012–2014	0.049	
CHBL	85.7	17	2012–2014	0.198	
SMSA	115.4	6	2012–2014	0.032	
SFCR	137.1	20	2012–2014	0.139	
SFMR	121.8	9	2012–2014	0.060	
Combined WSAs	548.5	59	2013–2015	0.108	This study
FARI	88.6	7	2013–2015	0.049	
CHBL	85.7	16	2013–2015	0.187	
SMSA	115.4	5	2013–2015	0.029	
SFCR	137.1	20	2013–2015	0.139	
SFMR	121.8	11	2013–2015	0.063	
Combined WSAs	548.5	58	2014–2016	0.106	This study
FARI	88.6	6	2014–2016	0.056	
CHBL	85.7	14	2014–2016	0.152	
SMSA	115.4	7	2014–2016	0.035	
SFCR	137.1	20	2014–2016	0.141	
SFMR	121.8	11	2014–2016	0.071	
Eldorado Density Study Area (EDSA)	355	49	1986–2014	0.076	*
EDSA– early period	355		1986–1988	0.072	Moen and Gutiérrez (1993)
EDSA – highest period	355		1995–1997	0.104	**
EDSA – most recent available	355		2012–2014	0.057	***
Yosemite NP	577	58	1988	0.101	Gould and Norton (1993)
Lassen	1889	71	2010	0.038	Keane (2010)

* Gutiérrez and Moen (1995, 1996); Gutiérrez and Seamans (1997); Gutiérrez and others (1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007b, 2008, 2009, 2010, 2011, 2012); Peery and others (2013, 2014, 2015).
** Gutiérrez and Moen (1996); Gutiérrez and Seamans (1997); Gutiérrez and others (1998).
*** Peery and others (2013, 2014, 2015).

streams and average elevation in the WSAs, and were weakly correlated with the average surface area ratio of the WSAs.

Discussion

This study described CSO occupancy in 5 mixed-ownership study areas with long histories of forest management, where timber has been harvested using a variety of methods. Through 5 y of concerted CSO surveys and population monitoring in our study areas, we detected additional sites, relatively high occupancy rates, and a range of crude densities. The CSO sites that were known prior to this study have persisted, and multiple CSO pairs breed in the heterogeneous landscape of habitats.

Centrally positioned among our study areas was the US Forest Service's EDSA, the location of a long-term CSO demographic study that has been collecting data since the 1980s. The EDSA is immediately north of the SMSA watershed (our lowest CSO density) and approximately 5 km southeast of the CHBL study area (our highest CSO density) (Table 4). Unfortunately, we cannot directly compare many of our results to those of the EDSA because of the different study periods, the lack of thorough WSA survey data from the 1990s, somewhat different survey methods (our 3 surveys per year versus their 4 surveys, and our activity-center searches), our lack of habitat-use data gathered by radio-telemetry, lack of comparable habitat data, and our lack of demographic data. With that caveat, we will point out several findings from the EDSA that, in combination with our results, may broaden the regional perspective on CSOs.

The EDSA annual reports (Table 4) did not elaborate on the amount of their survey effort that took place as walk-in surveys; therefore, we are uncertain whether our survey efforts are comparable. Farber and others (2012) and the

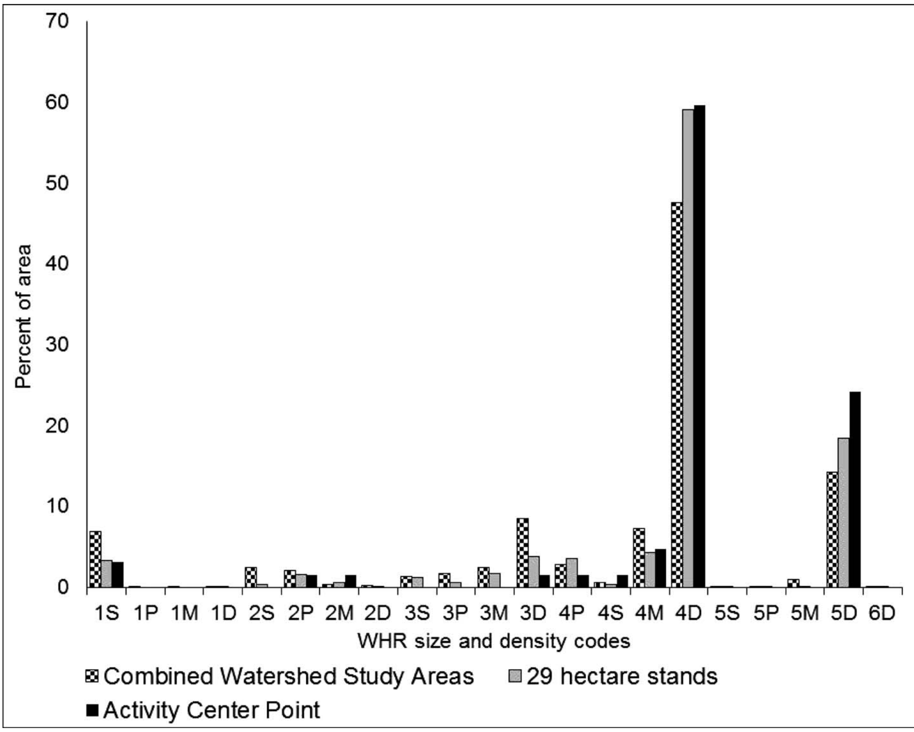

FIGURE 3. Percentage of WHR forest habitats (size and canopy closure) for the SPI watershed study areas at California Spotted Owl activity-center points ($n = 64$), 29-ha stands surrounding those points, and in all study areas combined, Sierra Nevada, California. WHR size and density codes: 1 = seedling <2.5 cm; 2 = sapling 2.5–15.2 cm; 3 = pole 15.2–28 cm; 4 = small tree 28–61 cm; 5 = medium-large tree >61 cm; 6 = multilayered, WHR 5S over WHR 4S or WHR 3S; S = 10–24%; P = 25–39%; M = 40–59%; D = 60–100%.

TABLE 5. Comparison of crude density of occupied California Spotted Owl sites to various factors at SPI's watershed study areas. Sierra Nevada, California.

Watershed study area (WSA)	CSO crude density sites km^{-2}	Total WHR 4M, 4D, 5M, 5D and 6 as proportion of WSA	Km of stream km^{-2} within WSAs	Weighted average elevation (m) of WSAs	Average surface area ratios of WSAs	Km of edge km^{-2} of WSA
FARI	0.049	0.739	14.391	1275	1.058	4.821
CHBL	0.187	0.937	9.547	1158	1.072	3.330
SMSA	0.029	0.725	11.187	1291	1.040	5.169
SFCR	0.139	0.645	7.112	975	1.046	5.239
SFMR	0.063	0.630	11.750	1356	1.071	5.914
		CSO density and proportion of WSA in primary habitat	CSO densities and stream km km^{-2}	CSO densities and weighted average elevation	CSO densities and average surface area ratio	CSO densities and edge
Correlation coefficient		0.563	–0.691	–0.680	0.398	–0.686
R^2 value		0.317	0.478	0.463	0.159	0.471

2012 protocol (USFWS 2012) state that higher occupancy rates can be obtained using activity-center searches. Additionally, the EDSA used a 4-visits-per-year protocol, whereas we employed a 3-visit protocol. The EDSA did not report their detection rates or survey results on a per-visit basis; thus no comparison or comment can be made regarding efficacy of their survey efforts.

In our WSAs, occupancy (both observed and estimated) was relatively steady or increasing during the 5 y of study. At the EDSA, occupancy was relatively stable during 2007–2015 (Jones and others 2016), but at a level that had declined by over 50% since the early 1990s (Peery and others 2013, 2014, 2015; Tempel and others 2014a).

Because we do not have data of similar quality for earlier periods in the WSAs, we cannot directly compare long-term trends in occupancy rates. We can only provide the intriguing observation that of the 45 sites in the WSAs that were known prior to 1996 (which were widely distributed among the WSAs), all but one were occupied at least once during 2012–2014. In seeming contrast, of the 44 sites known on the EDSA prior to 1996, only 22 were occupied at least once in 2012–2014 (CNDDB 2015). This seems strongly suggestive of an overall degree of stability in the WSAs that was not observed in the EDSA, but no further conclusions can be drawn.

Density is of course directly related to occupancy, because it is calculated based on numbers of sites. Reported densities from various CSO studies are compared in Table 4. Although long-term density on EDSA declined along with occupancy, from 2012 through 2014 the crude density of 0.057 occupied CSO sites km^{-2} at the EDSA was still well within the range of densities observed among the individual WSAs (although for a larger area than any single WSA) for the same period (Peery and others 2013, 2014, 2015). We do not have valid density estimates for the early 1990s at the WSAs, but even the high density of 0.104 sites km^{-2} reported for 1995–1997 at EDSA was within the range of densities reported for some individual WSAs in 2012–2016.

We found no strong correlations between the varying densities of owls and the landscape features we examined at the WSA scale. Perhaps our most unexpected findings were the weak positive relationship between CSO crude density and the percentage of primary habitat, and the weak negative relationship between CSO crude density and density of habitat edge (Table 5). Both appear inconsistent with findings at the EDSA, although we must acknowledge different analytical methods. We speculate that analyses at a more localized scale may yield more positive results as to the landscape features that CSOs are selecting in the WSAs.

Tempel and others (2014b) suggested that an average loss of 7.4% of high-canopy-cover forest in the EDSA territories between 1993 and 2012 may have contributed to the approximately 30% decline in abundance and territory occupancy. Their modeling indicated that medium-intensity harvest in the form of forest thinning was moderately associated with lower performance, but, "contrary to [their] predictions, the probability of a territory going extinct was reduced in proportion to the area harvested with high-intensity practices such as clear cutting and shelterwood harvest" (Tempel and others 2014b). The authors speculated as to increased prey production and availability near harvested areas, but stated that effect was rendered more uncertain because less than 6% of the area of the owl territories had been harvested intensively.

These findings suggest that some degree of intensive harvest may be favorable for CSO persistence. Since 1999, SPI has implemented an even-aged management strategy (clear cutting), removing high-canopy-cover forest and converting a portion of the landscape to rapidly growing early-successional forest. Since 1999, the proportion of SPI land on the landscape affected by clear cutting does not exceed 31% in any WSA. The resulting heterogeneity may be favorable for prey production, but this hypothesis has not yet been evaluated in our study areas.

Bias and Gutiérrez (1992) stated that CSO activity centers were not found on private lands in the EDSA, and Tempel and others (2014b) stated that private lands were used less than expected in the EDSA. Williams and others (2014) found foraging use to be less than available for private lands in an area of mixed ownership in the central Sierra Nevada, but did not specify the location. Our study demonstrates that these findings should not be generalized to broader areas; indeed, the WSA (SFCR) with the highest percentage of private lands had the 2nd highest crude site density even though it had the lowest proportion of primary habitat km^{-2} (Tables 1, 2, 5, 6). In contrast to other studies (Bias and Gutiérrez 1992; Williams and others 2014), the percentage of occupied sites on SPI lands was higher than the percentage of availability of such lands on 4 of our 5 study areas and slightly lower than availability on the 5th

TABLE 6. California Spotted Owl activity-center point locations on SPI, USFS, and other private lands within SPI's watershed study areas, Sierra Nevada, California.

Study Area	Number of occupied sites (2012–2016)		
	SPI	USFS	Other Private
FARI	7	2	0
CHBL	7	9	0
SMSA	5	2	0
SFCR	13	3	4
SFMR	8	3	1
Total	40	19	5
% occupied sites by ownership	62.5	29.7	7.8

(Tables 1 and 6). The percentage of occupied sites on federal lands was also higher than the percentage of availability on 3 of our 5 study areas and lower than availability on the 2 remaining areas. In all the WSAs, the percentage of occupied sites on all "other" lands was significantly lower than the percentage of availability.

Numerous factors could be positively or negatively affecting CSO populations at study areas across the Sierra Nevada region. The most visible factor might be the amount of intensive timber harvest being conducted on private lands. Since 1999, timber harvest methods have tended toward clear cutting on private lands and thinning on federal lands, but in each case, a minority of the landscape in the WSAs has been affected (Ed Murphy, Sierra Pacific Industries, Anderson, CA, pers. comm.; USDA Forest Service 2015a, 2015b). Contrary to conventional expectations and the claims of the recent listing petition (Sierra Forest Legacy and Defenders of Wildlife 2015), CSOs in the WSAs have persisted in proximity to relatively intensive forest management. Meanwhile the nearby EDSA population has reportedly declined in an area with limited forest management near the known sites and with larger protected areas (121-ha Protected Activity Centers).

From a broader view, the CSOs of the WSAs and the EDSA represent small but relatively well-studied portions of a Sierra Nevada metapopulation. The combined observations of these studies include different densities among various groups in time and space, different relationships to habitat conditions, and possibly, different population trends among adjacent areas. Different forest-management practices related to landownership have been suggested as key causal factors in these varied scenarios, but available data and analyses have not yet reached a level that adequately explains these differences. However, it is clear that stereotyping private lands as generally inhospitable to the CSO is inappropriate. Increasing our understanding of the ecology of the species and developing management tools will require a more nuanced approach.

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