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Basic principles of forest fuel reduction treatments

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Abstract

Successful fire exclusion in the 20th century has created severe fire problems across the West. Not every forest is at risk of uncharacteristically severe wildfire, but drier forests are in need of active management to mitigate fire hazard. We summarize a set of simple principles important to address in fuel reduction treatments: reduction of surface fuels, increasing the height to live crown, decreasing crown density, and retaining large trees of fire-resistant species. Thinning and prescribed fire can be useful tools to achieve these objectives. Low thinning will be more effective than crown or selection thinning, and management of surface fuels will increase the likelihood that the stand will survive a wildfire. Five empirical examples of such treatment are discussed: Hayfork fires, California, 1987; Tyee fire, Washington, 1994; Megram fire, California, 1999; Hayman fire, Colorado, 2002; and the Cone fire, California, 2002. Applying treatments at an appropriate landscape scale will be critical to the success of fuel reduction treatments in reducing wildfire losses in Western forests.

Keywords: Fire ecology; Fuel treatment; Prescribed fire; Thinning; Western United States

1. Introduction

Western forests are burning with uncharacteristic severity and scale. A significant contributor has been the paradox of successful fire exclusion: as we have become more efficient at suppressing wildfires, the wildfire problem has only become worse (Brown and Arno, 1991). In the past decades, several record years for wildfire area burned have occurred. Federal agencies have exhausted fire suppression funds during both 2002 and 2003, and the crisis has prompted a "healthy forests" initiative to address the problem (Bush, 2002). Although the problem is well defined in such policy documents, the solutions have remained diffusely defined, other than proposals that recognize that fuel reduction is needed at a scale unprecedented in US history. In this paper, we summarize a set of principles that will be important to address when fuel reductions of any scale are proposed. We provide examples through modeling and empirical evidence that restoration of more fire-resilient forests is possible. We define resiliency in this context as a forest capable of maintaining substantial live basal area after being burned by a wildfire. Just as importantly, we provide examples of forest management that will be ineffective in restoration.

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The history of the problem dates back to the early 20th century, when a fire exclusion policy was applied to all forests without regard to a context of place. Driven by the large 1910 fires in Idaho and Montana, the fledgling Forest Service lobbied Congress for legislation and funds to emplace sustainable forest management on the new national forests (Pyne, 2001). The policy included the suppression of all fires, as they were known to kill small trees and scar large trees reducing their commercial value (Show and Kotok, 1924). In the drier forests of the West, where fires were historically large but generally of low severity, the arguments of "light burners" who wanted to maintain fire as a natural process were snuffed out during the policy debates (Agee, 1993). A one-size-fits-all fire exclusion policy was applied to all forests. Protected forests soon had more tree regeneration (Benedict, 1930), and the early fires were easy to suppress with generally light fuel loading (Show and Kotok, 1929). Selective removal of large, fire-resistant trees added to the problem, so that by the late 20th century, we had widespread continuous forests with, on average, smaller trees and much greater fuel loads (Fig. 1). Areas that were once forest openings became forested (Skinner, 1995). Fires that once spread as surface fires were now more intense, and capable of jumping into the canopy of the forest as crown fires. This problem continues unabated into the 21st century, not only in high elevation or wet forests where that type of behavior was characteristic, but widely across all forest types (Covington et al., 1994; Hardy, 2005).

There is a critical need for widespread restoration of lower fuel amounts across the West. Yet fuels come in all shapes, sizes, and arrangements. There are live and dead fuels, herb and shrub fuels, litter, twigs and branches, ladder fuels (small trees), and canopy fuels (larger trees). A fuel reduction treatment might address any or all of these fuels, but depending on which are targeted, the treatment may not be relevant to either the easier suppression of unwanted wildfires, or the ability of the forest to sustain itself in the presence of wildfire.

2. Principles of fire resilient forests

The first principle to address in solving our widespread fuel problems is the context of place. This means that not every forest is a high priority candidate for treatment. Many forest types, including wet Sitka spruce, coastal Douglas-fir, and high-elevation forests such as mountain hemlock or subalpine fir, historically burned infrequently but with high intensity (Agee, 1993). Where trees that are 300–800 years old have never experienced a wildfire, it is difficult to argue that a serious fuels problem exists (Brown et al., 2004). There is certainly a lot of biomass on site, but much of it is unavailable for combustion under most conditions. Conversely, there are other forests that have long dry seasons each year and have easily combusted forest floors, such as ponderosa pine, mixed conifer, and drier Douglas-fir forests (Skinner, 2002), where the types of fires occurring today are very uncharacteristic of the historic fires. While some intense fire activity did occur in such forests, it was not the modal type of fire severity that exists today in such forests. There is broad consensus that active management of some type is needed in such forests (Allen et al., 2002; McKelvey et al., 1996), and that such treatment will be needed as a continued maintenance activity.

Broad scale, national assessments of fire risk have been made (Schmidt et al., 2002) but have been criticized as being too coarse. A finer scale classification based on potential vegetation (sensu Daubenmire, 1968) may be a more effective method to locally identify forests most at risk. Although the finest-scale classification unit is the plant association, aggregations of associations known as plant association groups (PAGs) are better planning units because they are of intermediate scale. These classifications are widely available across the West (e.g., Steele et al., 1981; Henderson et al., 1989; Atzet et al., 1996) and can be consistent with the coarser-scale national classifications. Where they do not work as well (as in parts of California) other fine-scale vegetation classifications may be utilized. While fuel treatments to address specific problems (such as the wildland–urban interface) may be appropriate in all forest types, large scale treatment of watersheds should receive highest priority in the drier forest types.

Once a context of place is defined, a set of "firesafe principles" can be defined (Table 1). Forests treated with these principles will be more resilient to wildfires. The principles are based on what we

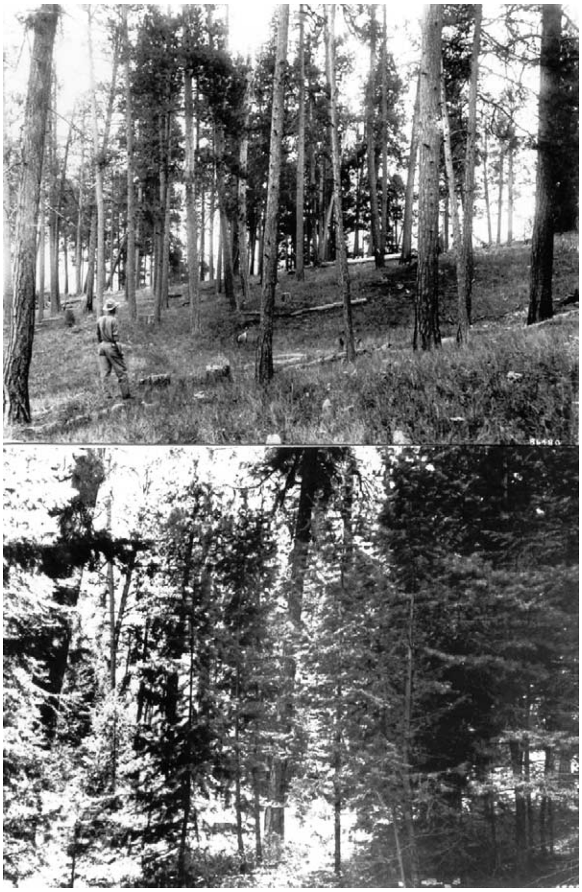

Fig. 1. Typical increase in surface fuels, ladder fuels, and canopy bulk density in a ponderosa pine forest, 1908–1948, in western Montana. Most of the historical trees are ponderosa pine, and most of the trees in the more recent photo are Douglas-fir. Photos from Gruell et al., 1982 (figure 19 p. 32).

currently know about crown fire. They occur when surface fires create enough energy to preheat and combust live fuels well above the ground. There are two stages to the crown fire process: the initiation of crown fire activity, known as ‘‘torching’’, and the process of active crown fire spread, where fire moves from tree crown to tree crown (Van Wagner, 1977; Agee et al., 2000).

Table 1
Principles of fire resistance for dry forests (adapted from Agee, 2002 and Hessburg and Agee, 2003)

Principle	Effect	Advantage	Concerns
Reduce surface fuels	Reduces potential flame length	Control easier; less torching[a]	Surface disturbance less with fire than other techniques
Increase height to live crown	Requires longer flame length to begin torching	Less torching	Opens understory; may allow surface wind to increase
Decrease crown density	Makes tree-to-tree crown fire less probable	Reduces crown fire potential	Surface wind may increase and surface fuels may be drier
Keep big trees of resistant species	Less mortality for same fire intensity	Generally restores historic structure	Less economical; may keep trees at risk of insect attack

[a] Torching is the initiation of crown fire.

Torching occurs when the surface flame length exceeds a critical threshold that is defined by moisture content in the crown and the vertical distance to live crown, called canopy base height or height to live crown. Moisture content of the crown is highest in the spring, particularly for new foliage, and declines to the level of older foliage (about 100% by dry weight, or equivalent to 1 g of water for each g of foliar dry weight) as the summer progresses (Agee et al., 2002). It is usually the late season moisture value that is used for planning purposes, so torching becomes primarily a function of canopy base height. At 100% foliar moisture, a 2 m canopy base height will require a flame length of 1.3 m to initiate torching, while a 6 m canopy base height will require a 2.8 m flame length (Agee, 1996).

Active crown fire spread begins with torching, but is sustained by the density of the overstory crowns and the rate of spread of the crown fire. The fire must consume a mass above a critical rate, known as mass flow rate, in order to sustain active crown fire. The critical mass flow rate has been defined as 0.05 kg m^{-2} s^{-1}, and is a function of the crown fire rate of spread (m s^{-1}) and the density of the crowns, known as canopy bulk density (kg m^{-3}). Canopy bulk density represents the mass of foliage in a given volume of crown, and is a stand-level variable, as contrasted to crown bulk density, which is the density within a single tree crown. A "crowning index" can be defined either as the minimum windspeed (an index to rate of spread) required to maintain crown fire activity, for a given canopy bulk density (Scott and Reinhardt, 2001) or alternatively, the minimum canopy bulk density under assumed worst case fire weather, where rate of spread is considered the "constant" (Agee, 1996). From a silvicultural perspective, the latter method is preferable, but requires assumptions about rate of spread, which are now based on a simple regression empirically derived from Rocky Mountain crown fires (Rothermel, 1991).

Although crown fire theory is largely based on boreal forest experiments and observations, it is nevertheless a useful tool is defining fire resilient conditions (Table 1). First, surface fire behavior must be controlled, so that treatments should either reduce such potential behavior or at least not contribute to increased fire behavior. Because such treatments often open the understory so that midflame windspeed will increase and fine fuel moisture will decline (van Wagtendonk, 1996; Weatherspoon, 1996), maintaining no change in surface fire behavior generally requires a reduction in surface fuels or significant greenup of grasses and low shrubs (Agee et al., 2002). Second, a reduction in torching potential requires a comparison of potential surface fire flame length with a critical flame length, which is a function of canopy base height. At best, a reduction in potential surface fire behavior plus an increase in canopy base height will minimize torching potential. Third, reduction in potential active crown fire spread can be accomplished by a reduction in canopy bulk density. Where thinning is followed by sufficient treatment of surface fuels, the overall reduction in expected fire behavior and fire severity usually outweigh the changes in fire weather factors such as wind speed and fuel moisture (Weatherspoon, 1996).

The fourth principle in a fire resilient forest strategy for the short-term is to keep the large trees in the stand if they are present. These are the most fire-resistant trees in the stand, as they have the tallest crowns and thickest bark (Peterson and Ryan, 1986). In the longer term, provision must be made for sufficient spatial variation in age classes to provide for replacement of the larger trees as they die. Where large trees are not present, and a thinning prescription is considered, the largest of the small trees should be reserved.

3. Creating fire resilient stands with fuel treatments

Application of these principles to forests clearly implies a three-part objective: reduce surface fuels, reduce ladder fuels, and reduce crown density. Prescribed fire is effective at surface fuel reduction (van Wagtendonk, 1996), and it can also increase canopy base height by scorching the lower crown of the stand. It is generally less effective at reducing canopy bulk density, as fires intense enough to kill larger trees often exceed the desired severity thresholds (Miller and Urban, 2000). Initial fires will consume substantial biomass, but will also create fuels by killing understory trees, so that surface fuel biomass may return to or exceed pre-burn levels within a decade, but with an increased canopy base height (Agee, 2003) (Fig. 2). Often, staged treatments

Fig. 2. Accumulation of dead material four years after a single prescribed fire following more than 70 years without fire in the Blacks Mountain Experimental Forest in northeastern California. Photo: C.N. Skinner, USDA Forest Service, Pacific Southwest Research Station.

of prescribed fires (Allen et al., 2002) can do an effective job of reducing fire hazard (McCandliss, 2002), particularly where canopy bulk density is already low enough that active crown fire spread is unlikely (e.g., stands in Fule et al., 2002).

Thinning is another silvicultural tool that may be effective in creating fire resilient stands (Graham et al., 1999), but it is no panacea. Consider three types of classic thinning: low, crown, and selection thinning (Fig. 3, Table 2). All three will reduce average canopy bulk density, but may not necessarily reduce the maximum canopy bulk density as calculated by the Scott and Reinhardt (2001) method. A textbook low thinning (Fig. 3) will simultaneously increase canopy base height, while crown and selection thinning will not. The latter two methods will generate more income, because they focus on larger trees (Hartsough, 2003), but large trees are also the most fire-resistant ones. In most dry forest stands (Figs. 1 and 4) there is often a thick, unmerchantable (<10 cm dbh) understory (three columns on the left, Fig. 4, comprising about 60% of the total tree stems), so that even a low thinning that ignores the smallest trees will not have much effect on canopy base height. With the unmerchantable material left on site, the low thinning is, in effect, a crown thinning. Subsequent treatment to remove smaller trees manually or with equipment can help reduce the unmerchantable material, but this adds expense to the operation.

Thinning will have either little effect or create an increase in surface fuels, depending on the method of yarding (Table 3). Whole tree harvest, with disposal of tops at the landing (chipping, burning) is most effective at preventing surface fuel increases in the residual stand, and helicopter yarding, the best system for minimizing immediate soil impacts from harvest, usually causes the highest surface fuel increases because tops from harvested trees are left in the woods. Harvester–forwarder operations increase surface fuels but concentrate and compact the fuels.

The influence of type of thinning and use of prescribed fire on stand survival after wildfire is illustrated by a simulation (Figs. 5 and 6) using fire behavior and effects models (NEXUS (Scott, 1999)) and First Order Fire Effects Model (FOFEM (Reinhardt et al., 2002)). A forest type with a historic low-severity fire regime (low elevation ponderosa pine/Douglas-fir/grand fir) and trees up to 100 cm dbh is subjected to thinning. The thinning reduces basal area from about 34 $m^2 ha^{-1}$ to about 14 $m^2 ha^{-1}$ (~60 $ft^2 ac^{-1}$), but several different types of thinning are applied: (1) no thin (the unharvested stand; (2) low

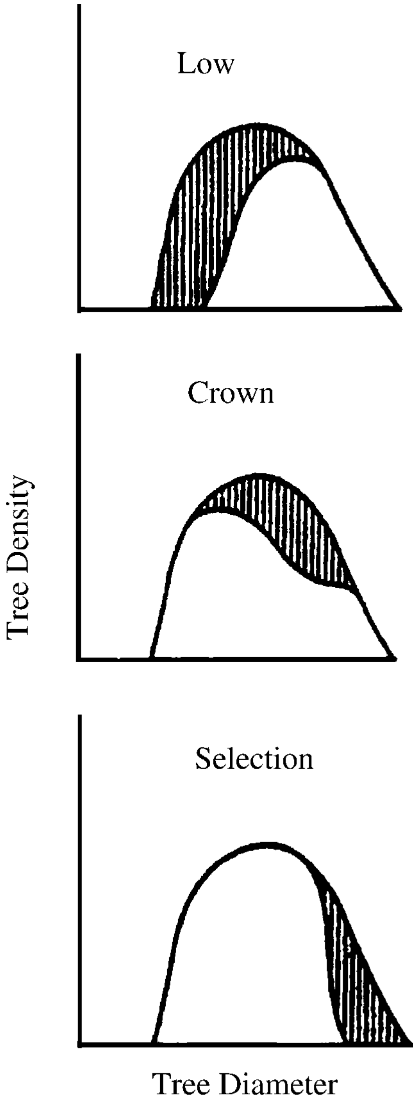

Fig. 3. Types of thinning in an even-aged stand. Low thinning removes trees from smaller diameter classes, crown thinning focuses on mid-canopy trees, and selection thinning focuses on the largest trees in the stand.

Table 2
Effect of thinning method on canopy characteristics

Method	Effect on canopy characteristics	
	Canopy base height	Canopy bulk density
Low thinning	I[a]	NE/D
Crown thinning	NE	D
Selection thinning	NE	D

I: increase; D: decrease; NE: no effect.
[a] If unmerchantable small trees also removed.

thinning where all small trees are removed, and cutting of successively larger trees continues until the basal area criterion is reached; (3) low thinning with a lower commercial size limit (15 cm), so the thinning begins with trees 15 cm and larger until the basal area criterion is reached; (4) selection thinning, where trees are removed from largest to smallest until the basal area criterion is reached; and (5) post-treatment prescribed fire where flame length is limited to 0.6 m. Although the vertical scales differ between the graphs in Fig. 5, quite different structures are created by the various treatment combinations, and they have differential survival in a severe weather wildfire simulated to occur after the treatments. Species composition is not shown, but is primarily ponderosa pine in the large size classes, with Douglas-fir in medium size classes and grand fir dominating the smaller size classes. Weather conditions for the simulated wildfire are described in Fig. 6, and mortality from surface fire was predicted from FOFEM using the predicted flame lengths. Where active crown fire was predicted, mortality was adjusted to 100% (Beukema et al., 2000), and where torching activity was predicted, mortality was adjusted up from the FOFEM prediction by the crown fraction burned.

The unmanaged stand (UM) was predicted to sustain active crown fire, and a stand replacement event was predicted (Fig. 6). Mortality was almost the same, but over a lower basal area, for the low thin with commercial limit (LT-CL) and the selection thin (ST) stand. In the former stand, the canopy base height was low, encouraging torching, and for the selection stand, no large, fire-tolerant trees remained. Where the selection thin stand was treated with prescribed fire, basal area was reduced by the fire but the stand did have some residual basal area after wildfire. Where small trees were removed, either by thinning or prescribed fire, survival after wildfire was a much higher proportion of total basal area (columns to right, Fig. 6). The unharvested stand that was treated with prescribed fire alone (UM/PF) lost some basal area, but its residual basal area after wildfire was above that of all the thinned stands. Any standing dead fuels created by the prescribed fire will, of course, fall to the ground (Fig. 2), and such future additions are not

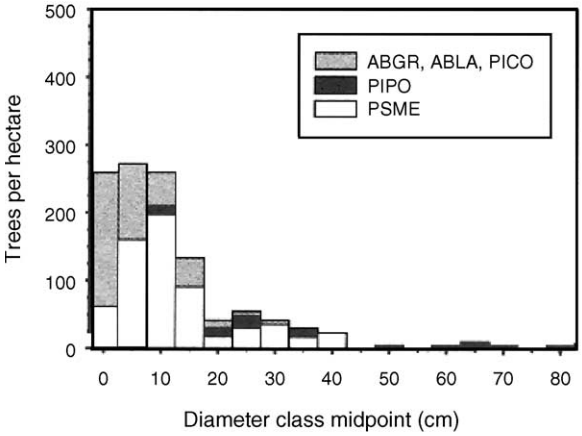

Fig. 4. Structure of a dry forest (from Scott and Reinhardt, 2001) indicating the predominance of very small, unmerchantable trees in the current structure (similar to bottom photo, Fig. 1. A low thinning of merchantable trees would begin at about 10 cm diameter, and crown or selection thinning would concentrate on even larger stems. Commercial harvest without treatment of the unmerchantable material will leave canopy base height unchanged and could increase surface fuel loads. ABGR = grand fir (*Abies grandis*), ABLA = subalpine fir (*Abies lasiocarpa*), PICO = lodgepole pine (*Pinus contorta*), PIPO = ponderosa pine (*Pinus ponderosa*), PSME = Douglas-fir (*Pseudotsuga menziesii*).

accounted for in these simulations. Within 5–10 years after treatment, potential surface fire intensity will increase where such fuels were created, although height to live crown will have been increased by the prescribed fire. A second prescribed fire treatment would be required in such cases to maintain low surface fuel loads.

If different stand structures or wildfire conditions were selected, the results shown would have varied somewhat, but likely remained in roughly the same order of effectiveness. The implications of these simulations are (1) Not every fuel reduction treatment will reduce fire problems. Treatments should be planned using principles of firesafe forests: treat surface fuels, ladder fuels, and although thinning of the crown may be desirable, leave large trees. Those treatments that focused on smaller trees and ladder fuels were effective, and prescribed fire alone was effective, too. (2) The conventional wisdom that under severe fire weather fuel conditions are irrelevant is not true: fuels and forest structure do make a difference (Agee, 1997). The large ponderosa pines all across the West in pre-fire-exclusion times attest to the fire resistance of those forests, which commonly burned over the centuries under severe fire weather as well as under more benign weather. Current stands with fire-resistant species, treated to reduce fire hazard, are also capable of surviving wildfires in worst case fire weather.

4. Empirical evidence for efficacy of fuel treatments

There is no opportunity to conduct experimental crown fire work in the dry forests of western North

Table 3
Effects of yarding method on surface fuel quantity and arrangement

Method	Effect on surface fuel amount/depth
Feller-buncher or cable/whole tree	NE/NE
Feller/buncher or cable/lop and scatter	I/I
Harvester–forwarder	I/NE or I/I
Helicopter	I/I

Whole tree yarding is usually restricted to ground-based methods; helicopter yarding leaves tops in the field. Surface fuel amounts: I: increase; D: decrease; NE: no effect. Surface fuel depth: I: increase; D: decrease; NE: no effect.

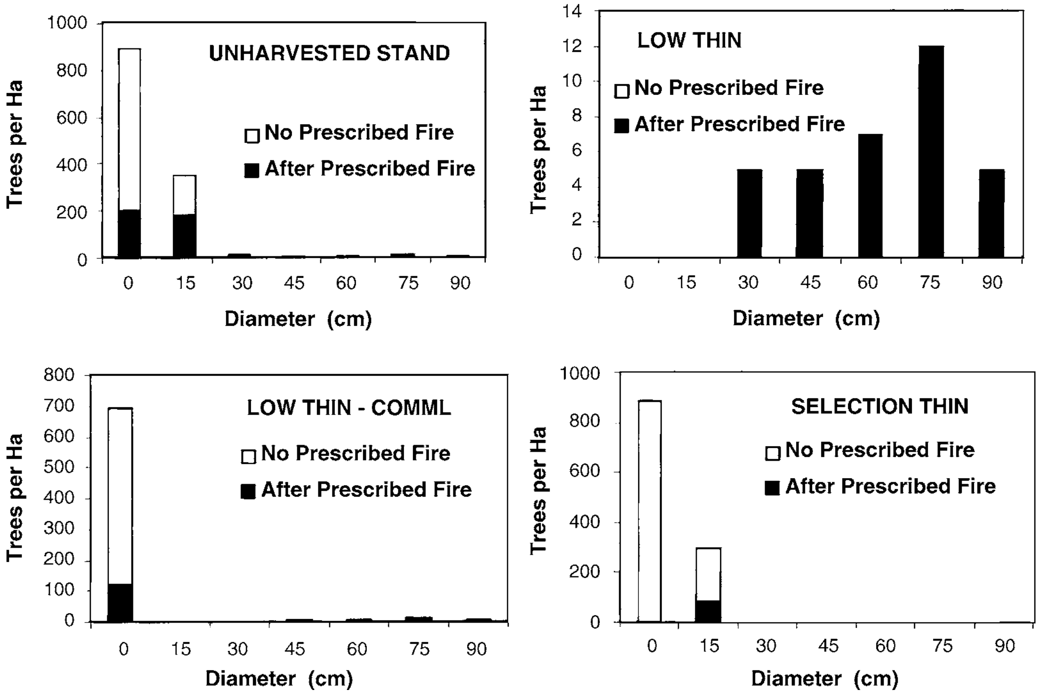

Fig. 5. Various forest structures created in the same stand by thinning, and thinning/prescribed fire. In each graph, the density of each size class after thinning is shown by the total height of the column. Structure after application of prescribed fire is shown in black. Note the vertical scales differ between each graph.

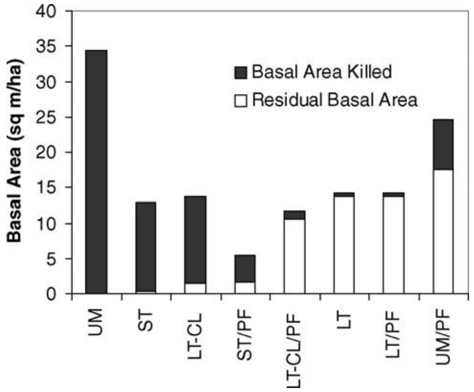

Fig. 6. Survival from a severe-fire-weather wildfire of the stand structures shown in Fig. 4. Columns are organized by absolute amount of residual basal area (white part of column). UM: unmanaged, ST: selection thin, LT: low thin, CL: commercial limit (>15 cm), PF: prescribed fire. The unharvested stand was assumed to be NFFL fuel model 10, harvested stands with no prescribed fire were assumed to be NFFL Model 11, and any stand treated with prescribed fire was assumed to be NFFL model 9. Fuel moistures for 1-, 10-, and 100-h fuels were 4, 5, and 6% for models 9 and 11 and 5, 6, and 7% for model 10. Open windspeed of 36 kph was adjusted to 0.4 for models 9 and 11 and 0.2 for model 10.

America. So possibilities of experimentally treating stands and then purposely subjecting them to a worst-case wildfire are non-existent. However, we do have the ability to observe wildfires as they move into previously treated stands, and although inference drawn from such events must be limited, such observations indicate that fuel treatment, scale, and time since treatment affect changes in wildfire behavior and effects.

4.1. Hayfork Fires, California, 1987

The Hayfork fires covered roughly 20,000 ha in 20 separate fires on the Shasta-Trinity National Forest in Douglas-fir dominated mixed-conifer forest, and were evaluated after the fact by Weatherspoon and Skinner (1995). “Treated” stands were not specifically treated for fire resiliency, as the stands were harvested largely via selective cutting of large trees, and fuel treatment after harvest was either lop and scatter or underburning. Severity was indexed by crown scorch. Uncut stands (generally old growth) had the lowest fire damage classes, because they contained the largest trees and had less surface fuel compared to stands with a harvest history. Yet, where logging had been followed by treating the surface fuels, the damage classes were not statistically different from the uncut stands (Weatherspoon and Skinner, 1995; Weatherspoon, 1996). The lesson here is that treatment without regard to residual fuel and forest structure, may exacerbate fire severity rather than ameliorate it.

4.2. Tyee Fire, Washington, 1994

The Tyee fire covered 50,000 ha on the Wenatchee National Forest. Small (5–20 ha) treated areas of second growth, which included 60-year-old mixed conifer forest, underburned while adjacent untreated areas of the same age burned with crown fires. The heated air created by the crown fires passed over the treated areas and scorched the tops of the trees that were later underburned. Many of these trees later died from the sandwiched scorch effect (Agee, personal observation), suggesting that scale of treatment is important. The Goman Peak fuelbreak (Fig. 7) created in the 1970s transformed a crown fire (coming from left) to a surface fire, which then became a crown fire again as it exited the fuelbreak. The trees in the fuelbreak had grown much larger than those in the untreated areas, which also helped their survival. However, many of the trees in the fuelbreak subsequently died, although the fuelbreak remains a green line up the hill. The lesson here is that scale matters: treatments with substantial edge adjacent to untreated units are likely to suffer substantial mortality, even if fire behavior is reduced.

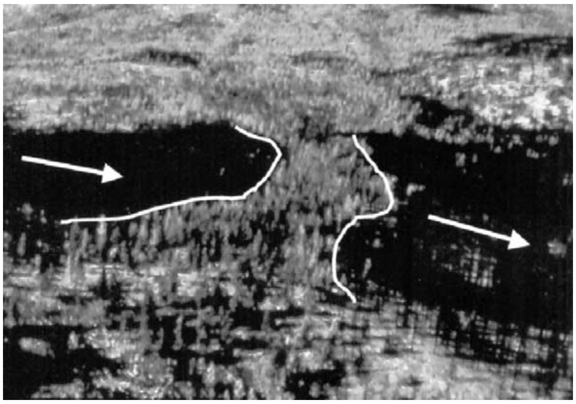

Fig. 7. Post-fire condition of the Goman Peak fuelbreak, Wenatchee National Forest, Washington. The crown fire came from the west (white arrow at left), moved as a surface fire through the fuelbreak (area bracketed by white lines), and then transitioned back to a crown fire to the east (white arrow at right) of the fuelbreak. Created in the 1970s, the fuelbreak received a low thin (to about 10 m^2 ha^{-1}), pruning to 3 m height, and pile burning of debris. USDA Forest Service photo.

4.3. Megram Fire, California, 1999

The 50,000 ha Megram fire burned on the Shasta-Trinity and Six Rivers National Forests in northwestern California in mixed-conifer forests dominated mostly by Douglas-fir. It burned through 12,000 ha of forest affected by a large windsnap–windthrow event in the winter of 1995–1996. Limited areas of 250-m wide fuelbreaks were established within these wind-affected zones, due to much of the area being within wilderness and administrative appeals on larger-scale fuel treatment. At least some of the fuel-treated area was reached after the main intense pulse of the fire subsided, and little to no suppression was attempted as the fires approached and entered the fuelbreaks. Stand replacement fires outside of the fuelbreaks quickly transitioned to surface fires in the fuelbreaks. Although crown scorch from heat generated in adjacent untreated forest did cause mortality on the windward side of some fuelbreaks, mortality was minimal by the time the fires reached the lee sides. Some effective fuelbreaks had only surface fuels and ladder fuels treated, with residual canopy cover exceeding 60–70% (Fig. 8). Even though canopy bulk density was insignificantly reduced, fire severity was significantly reduced, suggesting that reductions in canopy bulk density are not always needed to reduce wildfire severity.

4.4. Hayman Fire, Colorado, 2002

The 50,000 ha Hayman fire burned within the Pike-San Isabel National Forest southwest of Denver. It contained a major and severe fire run of 25,000 ha in 1 day. Many areas where fuels had been treated before the fire experienced lower severity effects than adjacent untreated areas (Finney et al., 2002). Fuel treatment was not always successful in reducing fire severity, particularly during periods of incredibly severe fire weather (winds to 135 kph (85 mph) and

Fig. 8. Example of a change in fire severity due to fuel treatment on the Megram fire. Upper left portion of photo is untreated forest that was affected by a windsnap event in 1996. Lower right is a fuel-treated area where surface and ladder fuels were removed. The fire burned in 1999. USDA Forest Service photo.

fuel moistures of below 6% in all size classes). Under less severe conditions, fuel treatments such as prescribed fire apparently altered fire severity, except where the treatments were of very small extent (less than 100 ha), or where they had been applied more than 10–15 years previously. Timber stand improvement work without treatment of fuels created by such activity were burned more severely than unmodified areas.

4.5. Cone Fire, California, 2002

The Cone Fire covered 800 ha and burned as a crown fire into the ponderosa pine dominated forests of the Black's Mountain Experimental Forest (BMEF) within the Lassen National Forest where it encountered three 100-ha stands experimentally thinned, or thinned and underburned (Oliver, 2000). Two stand structures were created in the BMEF project. One structure emphasized retaining the largest trees and is referred to as high structural diversity (HiD). The other structure removed the smallest and largest trees, leaving regularly spaced, intermediate sized trees, and is referred to as low structural diversity (LoD). For two of the stands (one LoD and the HiD) treatment had been completed 5 years previous to the Cone fire. Treatments had been completed in the third stand (LoD) two years before the fire. Each stand was split with surface fuels on one half treated with prescribed fire and the other half treated with lop and scatter. Where the Cone Fire encountered thinned and burned stands, the fire went out (Fig. 9). Where it encountered thinned stands with only lop and scatter of fuels created by the harvest, it burned as a surface fire with patches of scorched tree crowns in the stand. Though both the HiD and LoD treatments where prescribed fire had followed the thinning worked well in halting the high intensity fire, there were differences. The fire stopped at the edge of the LoD treatments. It continued as a very low intensity surface fire through needles up to approximately 100 m into the HiD stand before going out. The difference appears to result from the litter cast from the larger trees in the HiD stand, which covered the surface more completely than in the LoD stands (Skinner et al., in press).

Empirical evidence from other wildfires also supports the concept that forests treated with fire-hazard reduction objectives burn with less severity than adjacent untreated areas (Omi and Martinson, 2002; Pollet and Omi, 2002).

5. The challenges of temporal and spatial scales

Scale must be considered in restoring fire resistant forests. If fuel treatments are small and scattered, or a long time has elapsed since treatment (generally 10–15 years or more), they will be less effective in

Fig. 9. Left photo shows surviving trees in the half of Unit 46 that was thinned and burned. Right photo shows dead burned trees in the untreated area immediately adjacent to Unit 46. Both photos were taken back-to-back from same location on the treatment boundary. Photos: C.N. Skinner, USDA Forest Service, Pacific Southwest Research Station.

fragmenting the landscape fuel loads, and their efficacy at the stand level can be overwhelmed by intense fires burning in adjacent areas.

Temporal scale is not well understood, both for effective staging times for treatments and the length of time that treatments are effective. Thinning with fuel treatment is a ‘‘one-stop shopping’’ solution: bring the stand back into its natural range of variability in one operation (e.g., Fule et al., 2002). Allen et al. (2002), while noting a consensus for some action exists, cautions that staged treatments may be more effective. One example of staged treatment is the King’s River project on the Sierra National Forest, California, where some areas are being restored with prescribed fire alone. Most units are large (50–600+ ha), and of 5000 ha burned over 6 years, 35% has been reburned (McCandliss, 2002). Once initial restoration treatments are complete, length of effectiveness is likely a matter of place. Where fuels build up quickly, efficacy may be less than a decade (e.g., Brose and Wade (2002) in the southeast US). Observations of montane red fir ecosystems in Yosemite National Park where most natural fires are allowed to burn indicate that most natural fires have stopped at old fire boundaries up to 15-year old (van Wagtendonk, 1995). Fire histories in dry forests suggest that historical fires have occurred in successive years, and intervals as short as 3 years are not uncommon in ponderosa pine dominated stands, although the median or mean fire return intervals are often longer (Swetnam and Baisan, 1996; Heyerdahl et al., 2001). Such closely timed fires would almost certainly have been patchy and of low severity. McKenzie and Hessl (in press) present a neutral model of historical low-severity fire regimes that suggest both topography and fuels constrained historical fire spread.

Spatial scale of ecosystem treatment is also place-specific, whether prescribed fire alone or thinning plus fuel treatment is done. In the Sierra Nevada mixed-conifer type, some units are quite large (>600 ha; McCandliss, 2002), and this is true for the eastern Cascades mixed conifer type as well (Wenatchee-Okanogan National Forest). Median area burned by historical fire in the Klamath Mountains was slightly over 100 ha (Taylor and Skinner, 2003). The use of physical features such as streams and ridges (McCandliss, 2002) to design fuel treatments is consistent with natural fire boundaries (Taylor and Skinner, 2003). Constraints on the use of fire at coarse scale include air quality concerns and health effects on local residents.

Where thinning is used, there will be impact from the removal process. The soil impact of ground-based systems (Kellogg, 1995) will generally restrict extremely large-scale thinning operations. Silvicultural operations that have little soil impact usually have a negative fuels impact (e.g. helicopter yarding), but fuel increases can be ameliorated with prescribed fire. Existing road systems may not be entirely congruent with the needs for access for yarding, so that in some cases temporary road construction will be needed. Beginning in areas that are already appropriately roaded will limit the erosional impact of roads, and also introduce opportunities for rehabilitation or removal of old roads.

While the impacts of thinning and burning can be predicted, and may have some negative environmental impacts, these impacts need to be evaluated against the option of “no action”. “No action” is not a risk-free option, as dry climates regularly predispose forests to burn in a typical dry summer (Heyerdahl et al., 2001; Skinner, 2002; Swetnam and Baisan, 2003). The impacts of “no action” in dry forest ecosystems must incorporate the probability of stand-replacing, intense fire where stand density has increased and dead fuel accumulated in excess of historical levels. The probabilities of wildfire in space and time are not well defined: wildfire may not occur here this year, or there next year, but at some scale the spatial loss per time period can be defined. It may be quite difficult to point to a particular stand and define its probability of burning in some given future period, but the probability that substantial areas of dry forest will continue to be burned by severe wildfire is known, and it is high.

Very few landscapes will receive fuel treatment over the entire area, due to the constraints mentioned above as well as economic constraints. The landscape challenge is to define how much of a landscape needs to be treated, and where strategic fuel treatment will be most effective at reducing wildfire damage (Agee, 1996; Weatherspoon and Skinner, 1996; Taylor and Skinner, 1998). Some simulations of such work have been completed (Finney, 2001, 2003; Keane and Finney, 2003) and efforts are underway to apply these principles to real landscapes (Finney, Joint Fire Sciences Program, project in progress). The challenges are real, and become more important each year. Dry forests continue to burn at unprecedented rates, emplacing undesirable landscape patterns for a century or more, and reducing opportunities for restoration. Restoration activities are critical. We know what to do, and know, at least at a stand scale, how to do it right. Our greatest challenge is to expand that scale with socially accceptable treatments to sustain these dry forest landscapes into succeeding centuries.

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Ecology of the California Spotted Owl on the Lassen National Forest, 1990-2004; Final Report.

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INTRODUCTION

The California subspecies of the spotted owl (*Strix occidentalis occidentalis*) occurs in coniferous and hardwood forests of the southern Cascade Mountains of California, throughout the western slope of the Sierra Nevada, in the central and south coastal mountains of California, and into Baja California Norte, Mexico (Verner et al. 1992a, Gutierrez et al. 1995). The majority of California spotted owls occurs on public land in the Sierra Nevada and southern Cascades (Verner et al. 1992a).

This report summarizes fifteen years (1990-2004) of research on the California spotted owl on the Lassen National Forest. Our study was initially conducted through the U. S. Forest Service, Redwood Sciences Laboratory, in Arcata, CA (1990-1998). From 1999-2004, our study was conducted through Colorado State University, in Fort Collins, CO. As of 2005, this study became part of the California spotted owl module of the Plumas-Lassen Administrative Study, conducted jointly through Colorado State University and the U. S. Forest Service, Sierra Nevada Research Center, in Davis, CA.

Our original and primary objectives were to estimate demographic parameters including age-specific nesting and nest success rates, age-specific fecundity, age- and sex-specific survival rates, the finite rate of population change, and sex and age class structure of the population. Original objectives also included quantifying the spotted owls' diet through analysis of egested owl pellets, as well as characterizing nest trees and the composition and structure of vegetation surrounding nest trees. In 1998 we added two additional objectives to our study that were the subject of dissertation research by J. Blakesley: (1) Establish the relationship between demographic variation and variation in habitat structure and composition around spotted owl nest sites at multiple spatial scales (Blakesley 2003, Blakesley et al. In Press 2005), and, (2) Identify factors associated with spotted owl breeding dispersal probability and breeding dispersal distance and evaluate the consequences of breeding dispersal (Blakesley 2003, Blakesley et al. In Press 2006). In addition, we have documented the expansion of barred owls (*Strix varia*) and hybrid barred-spotted owls into northeastern California, and we have gathered data on external parasites of spotted owls. Finally, we collaborated on a study of spotted owl thermal ecology and energetics (Weathers et al. 2001).

Study Area

The Lassen study area encompassed approximately 2200 km^2 of National Forest land in northeastern California. The majority of the study area occurred on the Almanor and Eagle Lake Districts of the Lassen National Forest (LNF), with three owl sites on the Hat Creek District of the LNF and five sites on the Plumas National Forest. In addition, some owls were found on land immediately adjacent to the LNF which was owned or administered by private timber companies (nine sites), the National Park Service (three sites), the Bureau of Land Management (one site), or private individuals (one site).

In 2001, in response to a change in the method used to estimate population change (see below), we delineated a bounded study area encompassing the majority of owl territories containing banded owls (hereafter, Density study area, or DSA). The DSA consists of the geographic core of the study area. We based the DSA boundaries on topographic features (watershed boundaries) and administrative boundaries (e.g. between Forest Service and Private land). Sites not included in the DSA are located at the periphery of the Lassen study area, (e.g., in the northeast portion of the Eagle Lake Ranger District, on the Hat Creek Ranger District, on the north side of Lassen Volcanic National Park, and on the Plumas National Forest). Throughout this report, unless otherwise indicated, results are reported from throughout the greater Lassen study area.

Elevations on the study area ranged from 1200 to 2100 meters. Annual precipitation at the lower elevations averaged 141 cm in the west (Mineral, CA), 86 cm in the center (Chester, CA) and 36 cm just east of the study area (Susanville, CA). Most precipitation fell as snow between November and April. Average high temperatures in the center of the study area ranged from 6°C in January to 29°C in July. Average low temperatures ranged from -7°C in January to 7°C in July.

The study area lies at the southern end of the Cascade Geographic Province. However, it is included in the Sierra Nevada Province for spotted owl management purposes (e.g., USDA 1993, 2001, 2004, Verner et al. 1992a), as it lies at the northern limit of the distribution of the California spotted owl. The majority of forested stands on the study area were classified as white fir-mixed conifer ("mixed conifer") or red fir; both are typical of the Sierra Nevada (Rundel et al. 1977). Mixed conifer stands included white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*) and Douglas fir (*Pseudotsuga menziesii*). Red fir (*Abies magnifica*) stands were monocultures or contained occasional white firs.

FIELD METHODS

We followed standard techniques for locating, capturing, and banding spotted owls (Forsman 1983) and standard protocols for surveying large geographic areas, determining spotted owl reproductive status, and analyzing our data (Miller 1990, Franklin et al. 1996). Owls were initially located at night by vocally imitating their calls. When owls responded by calling back, we estimated each owl's location on a topographical map using one or more compass bearings taken from the observer to the calling owl. When an owl was detected, we conducted "walk-in" surveys to determine: (1) social status, i.e., whether the owl was single or paired with a mate, (2) reproductive status, and (3) identity of the owl. If an owl was unbanded or previously banded with a juvenile cohort band, we attempted to capture the owl and band it with a uniquely identifiable adult color band. In 1990 we began searching for owls at historic nest, roost, and nighttime detection locations, and added sites by surveying new areas.

We determined social status of non-juvenile owls (age ≥ 1 year old) on each visit; we made an overall determination of occupancy and social status for each site each year. In establishing pair status, a male and female owl had to be detected together on two or more occasions, with at least one pair detection occurring in the daytime (Franklin et al. 2004).

We determined owl reproductive status by following a standardized "mousing" protocol (Franklin et al. 2004) to eliminate observer bias in drawing conclusions about owl reproductive status. Mousing protocols are based on the owl's response to the presentation of live mice. In general, an owl belonging to a nesting pair will take mice to the nest; if fledged young are present, a parent will take mice to the young; if an owl is not nesting and no fledglings are present, the owl will eat and/or cache the mice.

We determined owl sex based on the pitch of their calls. We captured owls and banded them with unique color bands, or, if already banded, we identified owls by observation of the color bands. Whenever possible, we determined the age class of each owl (juvenile [young of the year], first year subadult, second year subadult, adult) based on plumage characteristics (Forsman 1981, Moen et al. 1991). We banded juvenile owls with a cohort (year-specific color) band that identified them as juveniles fledged in a specific year. When we subsequently relocated a subadult or adult owl wearing a juvenile band, we made a concerted effort to recapture it and band it with a unique color band. Each year, we attempted to locate and identify all subadult and adult owls which had color bands during the previous year and to capture all unbanded owls.

We delimited owl sites on the basis of nest and roost locations and the owls' behavior. Sites roughly approximated owl territories; territory boundaries, however, could not be determined without the use of radio-transmitters. Owl site centers often fluctuated between years, and some owls exhibited breeding dispersal (Blakesley 2003, see below).

From 1991-2000, we searched for each previously banded owl which we could not find, by conducting complete nighttime surveys of a 1.5 mile radius area centered around the owl's last nest or roost location. If an owl was replaced at a site by another owl of the same sex, we conducted two complete searches each year, for two years. If the owl had not been replaced, we conducted six visits to the site including four complete surveys each year, for two years. After an owl was missing for two years, we no longer conducted complete searches for that owl. From 2001-2004, rather than survey site-centered circles, we completely searched the Density Study Area at least three times each year.

We collected spotted owl pellets below roost and nest trees during daytime surveys. We also collected pellets whenever we observed a pellet being egested. Pellets were dried, stored, and later dissected to identify prey remains and consequently infer composition of the spotted owl diet.

We measured vegetation and physiographic characteristics surrounding nest trees. We established sampling strip plots 10 m in width, beginning 5 m from the nest tree and extending 30 m in each of the 4 cardinal directions. We measured diameter at breast height (dbh) and height of all trees ≥40 cm dbh, all snags ≥12 cm dbh, and all logs ≥25 cm diameter within the entire plots. We measured dbh and height of trees <40 cm dbh in the central third of each plot. We estimated canopy cover 10 m and 25 m from the nest tree in each of the 4 cardinal directions using a spherical densiometer. In addition, we recorded nest type (top cavity, side cavity, platform); species, dbh, and height of the nest tree; nest height; tree condition (live tree or snag); slope; aspect; and elevation.

SITE OCCUPANCY

Lassen National Forest personnel began surveying for spotted owls in 1981. Between 1981 and 1989, owls were detected at approximately 50 sites within the Lassen study area. We subsequently detected territorial owls at 115 sites from 1990 through 2004, including 78 territories within the Density study area (Tables 1 and 2).

Owl pairs occurred at 70 sites in the DSA and at an additional 26 sites in the Lassen study area in at least one year from 1990-2004 (Tables 1 and 2). Among the 78 sites within the DSA in which territorial owls were observed (Table 1), we compared site occupancy in 1991-1994 with site occupancy in 2001-2004. We observed declines between early years of our study and later years of our study, whether we compared the number of sites with any owl detection, at least one resident owl detection, or a pair detection (Table 3). These declines occurred despite more extensive surveys in 2001-2004 than in 1991-1994. Four spotted owl territories were abandoned following timber harvest within the nest stand (CARIBO, RUFFAR) or within approximately 0.5 km of the nest stand (GURNSE, COPPER). In addition, one territory (KAYTSA) was abandoned two years after the Storrie wildfire, even though the KAYTSA spotted owls nested in a charred snag the year following the Storrie fire.

Outside of the DSA, many sites where owls were found in earlier years were not surveyed in subsequent years because no owls were banded at those sites. Therefore, changes in the total number of sites where owls were found each year outside the DSA (Table 2) should not be interpreted as changes in spotted owl site occupancy over time.

REPRODUCTIVE RATES

Fecundity is defined as the number of female offspring per female owl ≥ 1 yr old. Productivity is the number of female offspring per female owl that produced young. We assumed ½ of all young were female.

Nesting rates were generally higher for adult than subadult female owls (Table 4). All measures of reproductive output showed considerable annual variation (Table 4). The proportion of female owls nesting ranged from 0.11 to 0.97. The proportion of nesting females that successfully fledged young ranged from 0.25 to 0.91. Fecundity of adult female spotted owls ranged from 0.07 to 1.09. Productivity of spotted owls ranged from 0.56 to 1.15. Estimated overall fecundity appears under “Fecundity, Survival and Population Change”, below.

The proportion of females nesting, productivity, and consequently fecundity were all higher in 1992 than in any other year. Over half of the broods observed in 1992 were composed of triplets, 7 sets of triplets were observed in 2002, and only one set of triplets was observed in the remaining years. The high reproductive output in 1992 and 2002 was reflected in increased recruitment in subsequent years -- a greater proportion of subadults were observed in 1993 and 2003 than in other years (Figure 2). The lowest number of subadults observed in the population, 2 in 1998, followed the year with the lowest fecundity--1997.

FLEDGING DATES

We observed 248 different broods of fledgling spotted owls in 1990-2004 (broods consisted of 1-3 young). Most fledging occurred in June, although fledglings were observed as early as 16 May, (*n* = 4 fledging events in May) and other nests were known to fledge from 1-17 July (*n* = 13). Of 128 nests known to be active ≤21 days before fledging was first observed, 90% fledged by 8 July (Figure 1).

FECUNDITY, SURVIVAL, AND POPULATION CHANGE – summary of peer-reviewed publications.

Analytical Methods

We analyzed spotted owl demographic rates from 1990-1999, including fecundity, age-specific apparent survival, and the finite rate of population change (λ; Blakesley et al. 2001). We estimated fecundity using mixed models ANOVA under a maximum likelihood framework (Littell et al. 1996), with owl site and year modeled as random effects. We estimated apparent annual survival probability using program MARK (White and Burnham 1999) and used QAICc in an information-theoretic framework to select the best model of survival probability (Franklin et al. 1996). We estimated λ using a four-stage projection matrix model (λ_{PM}; Caswell 1989, Franklin et al. 1996). We also conducted elasticity analyses to evaluate the contribution to λ of each fecundity and survival rate (Caswell 1989).

Projection matrices were used to estimate λ in three earlier meta-analyses of the northern spotted owl, *S. o. caurina* (USDI 1990, Forsman et al. 1996, Franklin et al. 1999), in two other studies of the California spotted owl (LaHaye et al. 1992, Seamans et al. 2001), and one study of the Mexican spotted owl, *S. o. lucida* (Seamans et al. 1999).

Projection matrix methods for estimating λ are based on several assumptions, including geographical closure (neither emigration nor immigration occurs) and a stationary population (average survival and fecundity rates occur each year). With respect to geographical closure, new owls are added to a projected population only through internal recruitment (using fecundity estimates), whereas owls are lost from the projected population through both death and permanent emigration from the study area (reflected in owl capture histories). Emigration is most likely to occur through natal dispersal. With respect to average vital rates, λ_{PM} is an asymptotic value that does not incorporate annual variation in survival and fecundity (see Franklin et al. 2004:17 and 53-54 for further discussion of the use of projection matrix population models with spotted owl data). It should be noted that the projection matrix method was the best available method for estimating λ during the time it was used by both northern and California spotted owl studies.

In July 2001 we participated in the first meta-analysis of demographic rates of California spotted owls, in Fort Collins, CO (Franklin et al. 2004). At this time, a new analytical method was available for estimating λ (Pradel 1996), referred to as the reparameterized Jolly-Seber method, or Pradel's model, and denoted as λ_{RJS} or λ_t. Pradel's model estimates λ directly from capture-recapture data, does not require the assumption of a stationary population and allows for time-specific estimation of λ. In a 1998 meta-analysis of the northern spotted owl, λ was estimated by both the projection matrix and Pradel methods (Franklin et al. 1999). Although the Pradel model was considered to be exploratory during the 1998 meta-analysis (Franklin et al. 1999), it was used exclusively in the 2004 northern spotted owl meta-analysis (Anthony et al. 2004) because it was considered to be more appropriate for spotted owl mark-recapture data (Franklin et al. 2004).

Estimates of λ_{PM} and λ_t. differ in their interpretation: λ_{PM} reflects whether the population of territorial female owls within a study area *are replacing themselves* (through internal recruitment) if the system was geographically closed, whereas λ_{RJS} reflects whether the population of territorial female owls *had been replaced*, from internal recruitment and/or immigration (Franklin et al. 1999, Franklin et al 2004). In both cases, $\lambda < 1$ indicates a declining population, and $\lambda > 1$ indicates an increasing population.

At the 2001 California spotted owl meta-analysis, we estimated fecundity using mixed models ANOVA under a maximum likelihood framework, with owl site and year modeled as random effects. We modeled even-odd year effects (alternating years of relatively higher and lower fecundity), linear effects of time (e.g., steady downward trend in fecundity over the years) and quadratic time effects (non linear trends in fecundity) and the combination of even-odd year effects and a linear trend. We estimated age-specific apparent annual survival probability in a meta-analysis, and λ_t for individual study areas and in a meta-analysis, using program MARK (Franklin et al. 2004). We used AICc and QAICc in an information-theoretic framework to model selection for selecting the most appropriate models of fecundity, survival, and population trend (Franklin et al. 2004).

Because a second meta-analysis of demographic rates for California spotted owls is scheduled for January 2006, we do not present new demographic analyses here.

Results

Fecundity

Least-squares mean estimates (± SE) of fecundity from 1990-1999 on the Lassen study area were 0.065 ± 0.066 for subadults (n = 33) and 0.291 ± 0.065 for adults (n = 381; Blakesley et al. 2001). Yearly effects accounted for 47% of the random variation in fecundity. In 2001, we were only able to compare models of fecundity among adult owls (n = 418). The best model of fecundity for the Lassen study area had an even-odd year effect ($\hat{\beta}$ = 2.96 ± 0.141) indicating higher fecundity in even-numbered years. This model was twice as likely as the next best model. Estimated mean fecundity across years (1990-2000) for adult spotted owls on the Lassen study area was 0.336 ± 0.083 (Franklin et al. 2004).

Apparent Survival Probability

We banded 219 juvenile and 200 subadult or adult owls at 90 sites, with a combined total of 1080 captures from 1990-1999. Estimated annual apparent survival probability ($\hat{\phi}$) was 0.333 ± 0.055 for juveniles and 0.827 ± 0.015 for subadults and adults combined (Blakesley et al. 2001). In the 2001 meta-analysis, we estimated survival for adult owls only, 1990-2000 (n = 223). The best model produced a combined estimate of apparent survival probability for the Lassen, Eldorado, Sierra, and San Bernardino study areas, $\hat{\phi}$ = 0.819 ± 0.008 (Franklin et al. 2004). From the best model that provided separate estimates for the Lassen study area (ΔQAICc = 5.53), $\hat{\phi}$ = 0.829 ± 0.015.

Population Trend

Using estimates of fecundity and apparent survival probability from 1990-1999, $\hat{\lambda}_{PM}$ was 0.910 ± 0.025, indicating an annual rate of decline in the territorial spotted owl population of 9% per year (Blakesley et al. 2001). Elasticity analyses revealed that λ was most sensitive to changes in survival of adult owls. However, the 43% of the variance in λ was due to variation in fecundity, and 28% due to variation in first year survival.

In the meta-analysis of λ_t we included capture histories of 191 adult and subadult spotted owls from 1992-2000, within a subset of the greater Lassen study area roughly equivalent to the current DSA described in the Field Methods of this report. The best model for the Lassen study area yielded $\hat{\lambda}_t$ = 0.985 ± 0.026 (Franklin et al. 2004). Due to constraints of the λ_t method, this estimate applied only to 1994-1999. Although there was no evidence for time-specific effects or time trends in λ_t when the Lassen data were considered alone, the top model from the meta-analysis of λ_t indicated annual variation in λ_t (Franklin et al. 2004).

Franklin et al. (2004:36) provided an important caveat in understanding λ_t:

> "Estimates of λ_t also should not be interpreted as numbers of birds; these are annual estimates of rates of change in the number of birds. For example, the periodic estimates of λ_t that are <1 in the SIE and LAS study areas represent a decrease in the number of birds. The intervening values >1 do not indicate that the population was restored to the original numbers at the beginning of the study; they only indicate that numbers increased relative to numbers in the preceding year. Thus, a cyclic pattern in λ_t can exist that ultimately results in losses of birds over time. However, this should be somewhat balanced in the estimates of mean λ_t over time."

In an effort to understand how λ_t affected changes in abundance, Franklin et al. (2004) estimated "realized population change" as the product of the annual estimates of λ_t. The resulting population trajectory for the Lassen study area showed a decline in abundance of spotted owls from 1994-1999; however, 95% confidence intervals were very large, indicating a fairly stationary population (Franklin et al. 2004).

Discussion

The even-odd year trend in fecundity among spotted owls in the Lassen study may be a characteristic of spotted owl populations in the Cascade geographic province; the even-odd trend was observed on all of the study areas in the Oregon and Washington Cascades (Franklin et al. 1999). This trend was also evident in the Lassen study area during the four years following the meta-analysis (Table 4).

Franklin et al. (2004:64) suggested that "the high reproductive output observed in 1992 may have affected rates of population change for several years following this event. If California Spotted Owl population dynamics were largely driven by such events, then continued monitoring of these populations will be necessary to capture these relatively rare events." We now have 4 additional years of site occupancy and fecundity data from the Lassen study area since the first California spotted owl meta-analysis. In 2002, we observed high reproductive output similar to that of 1992 (Table 4). However, site occupancy by resident owls in the Lassen study area did not rebound in the two years following this reproductive burst (Table-3).

Survival probability of adult California spotted owls on the Lassen and other National Forests was lower than survival probability of northern spotted owls where northern spotted owl populations were declining (Franklin et al. 1999).

Estimated λ_t from 1994-1999 (Franklin et al. 2004) was higher than estimated λ_{PM} from 1990-1999 (Blakesley et al. 2001) for spotted owls in the Lassen study area. Several explanations may account for the differences between the two estimates of λ from the Lassen study area, and these explanations are not mutually exclusive. First, recalling the differences in interpretation of the two estimates, the Lassen population may not be replacing itself but may be sustained by immigration from outside the study area. Second, the population may have declined more steeply from 1990-1994 than from 1994-1999. Third, the Lassen study was designed to use the λ_{PM} method and we did not completely survey the entire study area until 2001. This may have violated the assumption of equal capture probability of banded and unbanded birds required for estimation of $\lambda_{t.}$ If this assumption was violated, it would have positively biased the estimate of λ_t (Franklin et al. 2004). Finally, λ_{PM} may have been underestimated due to an underestimate of first year survival caused by emigration of juvenile owls from the study area. However, we believe the rate of juvenile emigration was relatively small because the Lassen study area is large relative to dispersal distances of spotted owls and our estimated apparent survival probability of juvenile owls (0.333 ± 0.055) was similar to that of an insular population of California spotted owls (0.344 ± 0.052; LaHaye et al. 1994).

DIET

We analyzed the contents of 3273 spotted owl pellets collected from 1990-2002. We estimated the biomass of each prey item consumed following standard methods employed for estimating spotted owl diet (e.g., Forsman et al. 2004). For this report, we estimated the average proportion of 10 prey categories across sites within each year, and then averaged the proportions across years.

Northern flying squirrels (*Glaucomys sabrinus*) accounted for 61% of prey biomass consumed. The remainder of the spotted owl diet was fairly evenly distributed among voles (8%; *Microtus spp.* and *Clethrionomys californicus*.), pocket gophers (8%; *Thomomys spp*.), woodrats (5%; *Neotoma spp*.), mice (5%; *Peromyscus spp*. and *Reithrodontomys megalotis*), birds (5%), diurnal squirrels (4%; *Sciurus griseus, Spermophilus lateralis, Tamiasciurus douglasii,* and *Tamias sp*.), shrews and moles (2%; *Scapanus latimanus, Sorex spp,* and *Neurotrichus gibbsii*), lagomorphs (2%; *Sylvilagus bachmani* and, possibly, hares), insects (<1%). Pellets also contained 7 bats, 2 lizards, and 1 snake.

The diet composition of owls throughout the Lassen study area in 1990-1992) was very similar to that reported for a smaller sample (geographically and temporally) from the Lassen study area reported in Verner et al. (1992b).

NEST TREES AND NEST STANDS

We measured nest stand characteristics for 132 spotted owl nests used on 174 occasions from 1990-2000 in the Lassen study area. Spotted owl nests occurred primarily in cavities of large live pines and firs (Table 5). Mean canopy cover in the immediate vicinity of the nest was consistently >80%. Nest tree dbh ranged from 38-219 cm; however, 90% of nest trees were ≥76 cm dbh. The number of hardwood stems was highly variable because very few sites contained a measurable hardwood understory, in contrast to some parts of the range of the California spotted owl (Verner et al. 2002a).

SITE OCCUPANCY, APPARENT SURVIVAL AND REPRODUCTION OF CALIFORNIA SPOTTED OWLS IN RELATION TO FOREST STAND CHARACTERISTICS – summary of peer-reviewed publication.

We evaluated the relationships between spotted owl demographic parameters and forest stand characteristics within spotted owl home ranges (Blakesley et al. In Press 2005). These analyses were predicated on the owls having selected home ranges within a landscape, and therefore reflect a finer scale of habitat selection than studies that compare habitat used with habitat available at a landscape scale.

Our objectives were to determine (1) whether variability in spotted owl site occupancy, apparent survival probability, or reproduction were related to forest cover and stand structure; (2) whether such relationships were stronger at the scale of home range core areas or at the scale of smaller nest areas; (3) which characterization(s) of high quality habitat best explained variation in site occupancy, apparent survival probability and reproduction; and (4) whether forest cover type, nest tree characteristics, and/or local nest stand measures were related to nesting success (Blakesley et al. In Press 2005).

Methods

We used vegetation classification maps for 67 spotted owl sites on and near the Almanor Ranger District of the Lassen National Forest, within roughly the western 2/3 of the Lassen spotted owl study area. Spotted owl data were collected as part of the Lassen spotted owl demography study. Measurement of vegetation and physiographic characteristics was described in Field Methods, above.

We defined spotted owl core areas (814 ha) following Bingham and Noon (1996). Core areas were empirically estimated regions within spotted owl home ranges that received concentrated use. Nest areas represented the area assumed to be used exclusively by a single owl pair. We defined nest areas (230 ha) based on one half the minimum distance between adjacent owl territories.

We modeled site occupancy as a function of habitat classes using logistic regression with an ordered multinomial response: no owls (0), single owl (1), owl pair (2) (n = 273). We used spotted owl capture history data from the demographic study to model the effects of vegetation covariates on apparent survival probabilities in program MARK (White and Burnham 1999). We modeled reproduction of adult female owls as a function of habitat classes using binomial logistic regression (no juveniles produced, including no breeding attempt and breeding failure [0], 1-3 juveniles produced [1]). We used logistic regression to model nest success as a function of nest tree and nest stand characteristics, habitat class of the nest stand, and year (*n* = 122 reproductive outcomes; 89 successes, 33 failures). For all analyses, we used an information-theoretic approach to model selection.

Results

Seventy-eight percent of the owl core areas and 83% of nest areas were composed of forested stands dominated by trees ≥30 cm dbh and with ≥40% canopy cover. Site occupancy was positively associated with the amount of the nest area dominated by large trees with high canopy cover within the nest area. Site occupancy was negatively associated with the amount of non-forested areas and forest cover types not used for nesting or foraging, and with medium-sized trees with high canopy cover within the nest area. Site occupancy also decreased over time and with increasing elevation. Apparent survival probability varied annually and was positively related to the area of each habitat class multiplied by the quotient proportion used/proportion available for each type, at both the nest and core scales. Reproductive output was negatively related to elevation and non-habitat within the nest area. Nest success was positively associated with the presence of large remnant trees within the nest stand (Blakesley et al. In Press 2005).

BREEDING DISPERSAL – summary of peer-reviewed publication.

Although spotted owls are generally philopatric, we observed breeding dispersal in 7% of inter-annual observations of banded individuals (*n* = 54 of 743 occasions; Blakesley et al. In Press 2006). We made a priori predictions about the factors associated with breeding dispersal probability, breeding dispersal distance, and the consequences of dispersal based on ecological theory and published literature.

Methods

We used logistic regression to model breeding dispersal probability as a function of sex, age class, reproduction, social status, territory quality, and interactions between territory quality and age class, territory quality and social status, and sex and reproduction. We used general linear models to model breeding dispersal distance as a function of age class, social status, sex, pre-dispersal territory quality and post-dispersal territory quality. In analyses of breeding dispersal probability and dispersal distance, we used an information-theoretic approach to model selection. We compared the quality of each owl's pre-dispersal territory with its post-dispersal territory. We compared the subsequent pair status of single owls that dispersed with single owls that did not disperse, using a X^2 test. Similarly, we compared the pair status of owls that lost their mates and dispersed with owls that lost their mates and did not disperse (Blakesley et al. In Press 2006).

Results

As predicted, breeding dispersal probability was higher for younger owls, single owls, paired owls which lost their mates, owls at lower quality sites, and owls which failed to reproduce in the year preceding dispersal. Breeding dispersal of northern spotted owls occurred at a similar rate (8%) and decreased with increasing age of the owls (Forsman et al. 2002). Sex had little effect on breeding dispersal probability in California spotted owls (Blakesley et al. In Press 2006), but was higher for female than male northern spotted owls (Forsman et al. 2002).

Breeding dispersal distance was similar for female and male California spotted owls (median = 7 km, range = 1-33; Blakesley et al. In Press 2006). In contrast, median breeding dispersal distances for northern spotted owls were approximately 14 km for males and 23 km for females (Forsman et al. 2002). We found no strong relationships between dispersal distance and any of the conditions that were associated with dispersal probability in California spotted owls (Blakesley et al. In Press 2006), whereas breeding dispersal distance was greater for younger than older northern spotted owls (Forsman et al. 2002).

Breeding dispersal resulted in improved territory quality in 72% of cases for California spotted owls, indicating that breeding dispersal is adaptive (Blakesley et al. In Press 2006).

NATAL DISPERSAL

Sixty-one owls banded as juveniles on the Lassen study area were reobserved in subsequent years, recaptured and given unique color bands (28 females and 33 males). Additionally, 12 owls with juvenile cohort bands were detected but were not recaptured. Straight line distances moved from natal sites to points of recapture ranged from 3 to 77 km (median = 25 km), with no differences observed between the sexes. Similarly, median natal dispersal distances of northern spotted owls were 25 km for females and 15 km for males (Forsman et al. 2002).

BARRED OWLS

A recent review of the status of the northern spotted owl thoroughly detailed the invasion and potential future threats of a close relative, the barred owl (Courtney et al. 2004). This report documented the rapid expansion of the range of the barred owl southward from Washington to include most of the historic range of the northern spotted owl. The report also documented negative interspecific interactions between barred owls and northern spotted owls including territory displacement, competition for food and space, and hybridization. Courtney et al. (2004) concluded that, although they were convinced that barred owls were negatively impacting northern spotted owls, additional data was necessary to address the extent of current and future potential impacts.

The first barred owl detection in California was in 1981 (Evens and LeValley 1982) and the range expansion since has been rapid (Dark et al. 1998). Although there are currently relatively few barred owl detections in the Sierra Nevada Mountains, the range is expanding (Courtney et al. 2004). Three barred owls have been detected on the Lassen study area. One was detected on a single occasion in 2001 and not captured. The other two occurred together during 2002 in the middle of a spotted owl territory that had successfully fledged three young. A female spotted owl was heard aggressively calling back and forth with a pair of barred owls on one occasion. Neither the adult spotted owls nor their young could be relocated later in 2002, despite numerous visits. We do not know if the spotted owls were silent or temporarily displaced. The same pair of adult spotted owls occupied the territory in 2003 and the barred owls have not been detected since.

We have also detected and banded three spotted owl/barred owl hybrids. Hybrid owls have not been detected in great numbers as the barred owl has expanded its range across the western United States and Canada (Courtney et al. 2004). Of 9000 *Strix* owls banded in Washington and Oregon, only 47 were confirmed hybrids (Kelly and Forsman 2004). One hypothesis is that hybrids occur mainly where barred owls are uncommon and finding a barred owl mate is difficult (Kelly and Forsman 2004).

The three hybrid owls we detected, two males and one female, have paired with spotted owls. None have successfully nested. All had plumage characteristics and vocalizations intermediate between spotted and barred owls, similar to previous descriptions of hybrids (Hamer et al. 1994). The first male hybrid detected was resident at an established spotted owl territory in 1999 and 2000 and was not detected after 2000. This male was observed on several occasions aggressively chasing and diving at the male and female spotted owls of a neighboring territory. Both the long-time resident female spotted owl where the male hybrid was present and the female spotted owl at the neighboring territory vacated their territories between the 1999 and 2000 field seasons, but returned after the hybrid male was gone. The second hybrid male was resident at an established spotted owl territory in 2001 but not detected after 2001. The female hybrid, the largest owl with the longest wing chord measured on our project, was first detected in 2001 and has been resident at three different established spotted owl territories in four years. This female was observed aggressively chasing a subadult female spotted owl that vacated the territory. The long-time resident female spotted owl formerly at the most recent territory used by the hybrid female owl later occupied a neighboring territory. Given overall low rates of breeding dispersal (see above), it is likely that the spotted owl was displaced by the hybrid owl. We believe that our observations support the idea that barred owls, and hybrids, aggressively displace spotted owls. Our study has the unique opportunity to examine the impacts of a potential invasion of the barred owl given a decade of pre-invasion information for comparison.

EXTERNAL PARASITES

Hippoboscid flies are a common ectoparasite on spotted owls (Young et al. 1993, Hunter et al. 1994) and can serve as vectors for pathogenic organisms (Baker 1967), including West Nile Virus (Gancz et al. 2004). With the recent arrival of West Nile Virus in North America and the possible susceptibility of spotted owls to West Nile disease, hippoboscids warrant increased attention by owl researchers and managers (Courtney et al. 2004).

Young et al. (1993) found that handling of spotted owls during capture was 95% efficient in detection of hippoboscid flies, and reported 17% of northern spotted owls in northwest California were infested with hippoboscids. We have observed hippoboscid flies on 2.3% of owls captured (n = 689). Only two juveniles that we captured had hippoboscid flies (n = 353). Young et al. (1993) also found that juveniles had a much lower rate of infestation than adults and noted that this may be due to lack of protection from preening in juvenile plumage. Young et al. (1993) did not compare infestation rates of subadult and adult spotted owls; however, we found subadults had a 7.3% infestation rate (n = 96) whereas 2.3% of adult owls were infested (n = 216).

We have not taxonomically identified the hippoboscids from the Lassen study area but we have collected and preserved the majority of hippoboscids encountered. We have not observed any other external parasites on spotted owls in the Lassen study area.

THERMAL ECOLOGY AND ENERGETICS – summary of peer-reviewed publication.

We collaborated on a study of the thermal ecology and ecological energetics of California spotted owls (Weathers et al. 2001). The study measured spotted owl resting metabolic rates using open-circuit respirometry in the laboratory, and field metabolic rate using the doubly labeled water technique. Results indicated that spotted owls have a basal metabolic rate of 10.13 ± 0.46 J/g/hr and a thermoneutral zone of 18-35ºC. The basal metabolic rate was only 82% of that predicted allometrically. Estimated field metabolic rate of adult spotted owls with dependent young averaged 249 ± 60 kJ/day, only 34% of that predicted for similarly sized non-passerine birds (Weathers et al. 2001).

Resting metabolic rate of spotted owls at temperatures above 35 ºC increased 1.5 times faster than predicted allometrically, supporting the hypothesis that spotted owls prefer structurally complex, older forests because of the forests' favorable microclimate (Weathers et al. 2001).

SUMMARY

In 15 years of research, we have provided insight into many aspects of California spotted owl ecology, including demographic rates and trends, relationships between demographic parameters and forest stand characteristics, causes and consequences of breeding dispersal, diet, competitors, parasites, and energetics. We have published 5 peer-reviewed papers; readers are encouraged to read our publications for more complete understanding of our analyses and results.

Key findings of our research include:

- Several lines of evidence suggesting the spotted owl population in the Lassen study area declined from 1990-2004. The number of sites occupied by territorial owls declined, two estimates of population change (λ) were < 1, and models of site occupancy in relation to habitat included a declining trend over time. There is no evidence that the spotted owl population on the Lassen study area increased from 1990-2004.

- Site occupancy and apparent survival of California spotted owls were enhanced in core and nest areas that contained habitat features known to be selected by the owl at the landscape scale. Reproductive output decreased as the amount of non-habitat within the nest area increased.
- Diet of spotted owls in the Lassen study area is dominated by a single prey species, the northern flying squirrel.
- Breeding dispersal probability was higher for younger owls, single owls, paired owls which lost their mates, owls at lower quality sites, and owls which failed to reproduce in the year preceding dispersal. Breeding dispersal resulted in improved territory quality for most owls.
- Barred owls and hybrid barred x spotted owls were rare on the Lassen study area through 2004. However, barred and hybrid owls appeared to displace territorial spotted owls.

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Table 1. Social status [a] of California spotted owls within the Lassen Density study area, 1990 through 2004.

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
ALDERC	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
BATTLE	NS	NS	NS	NS	NS	NS	PAIR	MRFP	PAIR	PAIR	PAIR	MRFP	0	0	0
BENKNO	MR[b]	MR[b]	MP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR
BENNER	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	FP	PAIR	MP	0	0	0	0	0	0
BENSPR	0	0	0	FR	0	0	MR	0	MR	0	0	PAIR	PAIR	PAIR	PAIR
BLULED	NS	NS	NS	MRFR	NS	MRFR	PAIR	MRS	MRFP	MRFR	MPFP	0	0	0	0
BOGARD	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
BUTTCR	PAIR	MRFR	PAIR	PAIR	MRFR	PAIR	PAIR	MRFP	PAIR	MRFR	0	MRS	MRFP	MRFP	PAIR
BUTTMN	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	MPFR	0	0	0	0	MP
BUTTMW	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
CAIRNN	PAIR	PAIR	PAIR	PAIR	MRFP	0	MRFP	0	0	0	FP	0	MP	MP	PAIR
CARIBO	PAIR	PAIR	PAIR	0	0	NS	0	0	0	0	0	0	0	0	0
CARTER	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FRS	0
COLDCR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0
CONELA	NS	MR	NS	0	0	MP	0	0	0	0	0	0	0	0	0
COPPER	PAIR	PAIR	PAIR	PAIR	0	MPFP	0	0	NS	0	FRS	MP	0	MRS	0
CRAZYH	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	PAIR	PAIR	PAIR	PAIR
CUMMIN	PAIR[b]	MPFP[b]	FP[b]	MP	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR
DOEMTN	NS	NS	NS	NS	NS	NS	PAIR	MPFR	NS	FP	NS	NS	FR	MRFP	PAIR
DOMING	NS	NS	NS	NS	NS	MR	NS	NS	NS	NS	NS	NS	0	0	0
DYERMT	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FRS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
EAGLER	NS	MRFP	PAIR	NS	NS	NS	NS	NS	NS	NS	NS	NS	0	0	0
ELAMCR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
ELAMEA	NS	NS	PAIR	PAIR	MRFR	MRFR	0	0	0	0	0	0	0	0	0
ELAMWE	NS	NS	NS	NS	NS	MR	0	0	0	0	0	0	0	0	0
FANANI	MRFP	PAIR	MRS	PAIR	MPFP	0	NS	NS	0	NS	NS	NS	0	0	MRFP
FANSOU	NS	NS	NS	PAIR	MPFR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
FLEISH	PAIR	MR	PAIR	MRFP	PAIR	PAIR	PAIR	MRS	0	MRFP	MRS	0	0	0	0
GRIZZL	PAIR	PAIR	PAIR	MPFP	NS	NS	NS	MPFP	NS	NS	NS	NS	MPFP	NS	NS
GURNSE	NS	MRFP	PAIR	PAIR	PAIR	0	0	0	NS	0	0	0	0	0	0
HAMILT	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR
HAMPTO	MPFP	MP	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	0	MP	0
HAZENF	NS	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	NS	PAIR	PAIR	MRS
HOLEGR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR
JENNIE	PAIR[b]	PAIR[b]	PAIR	MRFR	MRFP	MPFP	PAIR	PAIR	PAIR	0	PAIR	PAIR	PAIR	PAIR	PAIR
KAYTSA	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0
LASTCR	NS	MR	PAIR	PAIR[b]	MRFR	MRFR	PAIR	PAIR	0	0	0	0	0	FP	0
LCSPRS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
LGRIZC	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	MRS	MRS	PAIR	PAIR	0	PAIR	MRS	MRFP
LOCHER	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
LONGVI	NS	PAIR	PAIR	PAIR	PAIR	MRFP	0	0	0	MP	0	0	0	0	0
LOSTTO	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	MRS	0	MP	0	0	0	MPFP	0
MARNOR	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR
MARTIN	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR
MILLCR	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FP	PAIR	PAIR	PAIR
MILLER	MP	MP	MR	MRFR	PAIR	MRS	0	0	MRFP	MRS	0	MP	0	0	0
MOONPA	PAIR	PAIR	NS	0	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	0

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
MORGAN	MRFP	PAIR	PAIR	PAIR	MR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
MOSQUI	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
MUDCRE	PAIR	PAIR[b]	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	0	0	0	0
PEAPTN	MRFR	MRFR	NS	NS	MR	NS	MR	0	0	0	0	0	0	MRS	0
PEGLEG	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	PAIR	FP
PINECR	NS	NS	NS	MRFR	MRS	PAIR	MRS	MP	NS	0	0	FP	PAIR	MRS	MP
RICECR	MP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
ROCKCR	PAIR[b]	MRFP[b]	PAIR	PAIR	MPFR	PAIR	FP	NS	FP	PAIR	FP	0	0	MRS	FP
ROCKPT	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
RUFFAR	NS	MRFP	0	NS	NS	NS	NS	PAIR	PAIR	PAIR	0	MRS	0	0	0
SCENIC	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR
SHANGH	MRFP	MRFR	0	0	NS	0	MP	NS	0	NS	NS	NS	0	0	0
SHANOR	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR
SMBUTT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0	MPFP	0
SOLDIE	NS	NS	NS	NS	NS	MRFP	MP	MP	NS	NS	NS	NS	0	MP	0
SPENCE	NS	NS	NS	NS	NS	0	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	0	0
STARBU	PAIR[b]	PAIR[b]	PAIR[b]	PAIR[b]	MRFP[b]	MR[b]	NS	NS	NS	NS	NS	NS	0	FP	0
SUSNRN	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
SWAINM	NS	NS	NS	NS	NS	NS	PAIR	PAIR	MPFP	0	0	0	0	0	0
TURNER	MR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	FRS
TWINTS	PAIR	MRFR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	MRS	0	MPFP	MPFR	0	0	0
UPDEER	NS	NS	NS	NS	NS	MRFR	FP	NS	NS	NS	PAIR	NS	MPFP	PAIR	PAIR
UPSTEP	PAIR	FP[b]	NS	PAIR	MRS	PAIR	0	0	MRFP	MRS	MRS	PAIR	0	0	0
UPYELL	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	MPFR	PAIR

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
WARNER	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	MRFP	MRS	MP	0	0
WARVAL	NS	NS	NS	NS	PAIR	0	0	NS	NS	NS	NS	NS	0	0	0
WILDCM	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	NS	0	0	0	0	0	MP
WILLAR	MPFP	MPFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	MRFP	PAIR
WILLKS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
WILLOW	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
WILSON	MPFR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
CLOVER[c]												0	0	FP	0
FEATHE[c]				MP								0	0	0	0
JONESVA[c]						MP						0	0	0	0
LTFRED[c]												0	0	MP	0
MILRES[c]												0	0	FP	UP
SLATEC[c]												0	0	FP	0

[a] Key: M = Male; F = Female
R = Owl Resident (detected at least 2 times, separated by one week)
P = Owl Present
PAIR = Male and Female Resident, found together at least twice
S = Resident owl is confirmed to be single (no owl of the opposite sex detected after 6 visits)
NS = Not Surveyed completely
0 = Surveyed completely and no owls detected
UK= Owl of Unknown sex detected (did not vocalize)

[b] One or more owls carrying a radio transmitter; not used for demographic estimates.

[c] Owl observed on only one occasion/yr; not an established territory.

Table 2. Social status [a] of California spotted owls within the greater Lassen study area but outside of the Density study area, 1990 through 2004.

Site	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
ALDCAM	NS	NS	NS	NS	NS	NS	MRFP	PAIR	PAIR	MRFR	MRS	PAIR	MPFP	MPFP	NS
ASHURS	MRS	NS	NS	NS	NS	MR	NS	NS	NS	NS	NS	NS	NS	NS	NS
BATHTU	NS	PAIR	NS	NS	NS	NS	MRFP	PAIR	MP	NS	NS	NS	NS	NS	NS
BATHTW	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MP	NS
BAXTER	PAIR	PAIR	PAIR	PAIR	PAIR	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS
BEARFL	NS	MRFP	0	FP	0	0	NS	NS	NS	NS	NS	NS	NS	NS	NS
BIGBEN	MPFP	FP	NS	NS	NS	NS	NS	PAIR	MRFR	MRFR	PAIR	MR	NS	NS	NS
BLACKS	NS	NS	NS	NS	MPFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CAMPBE	NS	NS	NS	NS	NS	NS	MR	MR	NS	PAIR	MRS	MRS	NS	NS	NS
CANDAM	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	NS	NS	NS	MP	NS	NS
CHRISH	FRS	0	PAIR	MR	MP	MR	MP	PAIR	NS	NS	NS	NS	MRFR	0	0
CRATER	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	0	PAIR	PAIR	PAIR
CUBCRE	MR	PAIR	MPFP	MRFP	MRFP	MRFR	FP	NS	NS	MPFP	MPFP	0	0	MP	NS
FANLAV	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	NS	NS
GOLDRU	PAIR	PAIR	PAIR	PAIR	0	MP	MP	0	NS	0	0	0	0	0	NS
GRAYSF	NS	NS	NS	NS	NS	MR	NS	NS	MP	NS	NS	NS	NS	NS	NS
HEARTL	PAIR	PAIR	MR	MRFP	NS	NS	NS	NS	NS	NS	NS	NS	MPFP	NS	NS
HUMBOL	MRFP	0	NS	MPFP	NS	NS	NS	NS	NS	MR	NS	MP	NS	NS	NS
JENNCR	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
KEDRTS	PAIR	PAIR	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
KEDSOH	NS	MPFP	NS	NS	NS	NS	NS	NS	MPFP	NS	NS	NS	NS	NS	NS
LASTCH	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	NS	NS
LCWEST	NS	NS	NS	NS	NS	MPFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	NS	NS
LIGHTS	NS	NS	NS	NS	MRFR	NS	NS	NS	NS	MP	NS	MR	NS	MPFR	NS
LOGANM	MRFR	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	0	0	FRS	NS
MONTPT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	FP	MRFP	MRFR	PAIR
MOSRID	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	MPFP	PAIR	PAIR	PAIR	NS
MUDBUT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR
MUDSOU	NS	NS	NS	FR	0	0	NS	NS	NS	NS	0	0	0	0	0
PCTRAI	MPFP	MPFR	PAIR	MRFR	PAIR	FP	FP	0	0	NS	NS	NS	0	0	0
PEASOH	PAIR	MRFP	PAIR	MPFR	MRFR	MR	MR	MR	0	MRS	FRS	0	0	0	MP
PHILBR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	MRFP	NS	NS	NS
REESEF	MPFP	MRFP	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ROOPMT	NS	NS	PAIR	MRFP	PAIR	PAIR	PAIR	MRFP	0	0	0	NS	NS	NS	NS
SODARI	MP	MRFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
SODRAV	NS	NS	NS	NS	NS	NS	MRFP	MR	MR	MRFP	PAIR	PAIR	PAIR	NS	NS
WHEELE	NS	NS	PAIR	0	0	0	NS	NS	NS	NS	NS	FP	NS	NS	NS
COLBYC[c]	NS	NS	NS	NS	NS	FP	NS	NS	NS	NS	NS	NS	NS	NS	NS
HOMERL[c]	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
LNPSTA[c]	NS	NS	NS	NS	NS	FP	NS	NS	NS	NS	NS	MP	NS	NS	NS
MARSPR[c]	NS	NS	NS	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	NS	NS

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
MOONPK[c]	NS	NS	NS	NS	NS	MP	NS	NS	FP	NS	NS	NS	NS	NS	NS
SQUIRR[c]	NS	MP	NS	FP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[a] Key: M = Male; F = Female
R = Owl Resident (detected at least 2 times, separated by one week)
P = Owl Present
PAIR = Male and Female Resident, found together at least twice
S = Resident owl is confirmed to be single (no owl of the opposite sex detected after 6 visits)
NS = Not Surveyed completely
0 = Surveyed completely and no owls detected
UK= Owl of Unknown sex detected (did not vocalize)

[c] Owl observed on only one occasion/yr; not an established territory.

Table 3. Changes in spotted owl site occupancy over time on the Lassen Density study area (DSA). These data are derived from Table 1.

Number of sites among 78 established territories in the DSA	1991	1992	1993	1994	2001	2002	2003	2004
Pair detected	40	49	45	36	30	38	33	34
At least 1 resident owl detected	53	51	54	52	41	40	44	38
Any owl detected	58	53	56	53	45	44	51	43

Table 4. Reproductive rates of California spotted owls on the Lassen study area, 1990-2004. Fecundity is the number of female offspring per female owl ≥ 1 yr old. Productivity is the number of female offspring per female owl that produced young. We assumed one half of all young were female.

	Female	Females nesting		Nests successful		Fecundity		Productivity	
Year	Ageclass	Proportion	n	Proportion	n		n		n
1990	Adult	0.76	21	0.69	16	0.35	30	0.70	15
	Subadult	0	4		0	0	4		0
	Unknown		0		0	0.50	4		2
	Total	0.64	25	0.69	16	0.33	38	0.74	17
1991	Adult	0.39	28	0.55	11	0.19	35	0.81	8
	Subadult	0	1		0	0	2		0
	Unknown	0	1		0	0	1		0
	Total	0.37	30	0.55	11	0.17	38	0.81	8
1992	Adult	0.97	37	0.92	36	1.09	49	1.19	45
	Subadult	1.00	1	0	1	0.33	3	0.50	2
	Unknown		0		0	0.50	1		1
	Total	0.97	38	0.89	37	1.04	53	1.15	48
1993	Adult	0.66	29	0.68	19	0.38	33	0.78	16
	Subadult	0.17	6	1.00	1	0.06	9	0.50	1
	Unknown		0		0	0	1		0
	Total	0.57	35	0.70	20	0.30	43	0.76	17
1994	Adult	0.36	28	0.80	10	0.28	36	0.83	12
	Subadult	0	5		0	0	6		0
	Unknown	0	2		0	0	3		0
	Total	0.29	35	0.80	10	0.22	45	0.83	12
1995	Adult	0.33	36	0.58	12	0.13	46	0.75	8
	Subadult		0		0	0	1		0
	Unknown		0		0		0		0
	Total	0.33	36	0.58	12	0.13	47	0.75	8
1996	Adult	0.38	32	0.58	12	0.19	40	0.83	9
	Subadult	0	1		0	0	1		0
	Unknown		0		0		5		2
	Total	0.36	33	0.58	12	0.20	46	0.82	11
1997	Adult	0.17	30	0.40	5	0.07	36	0.83	3
	Subadult	0	2		0	0	3		0
	Unknown	0	4		0	0	6		0
	Total	0.14	36	0.40	5	0.06	45	0.83	3
1998	Adult	0.86	21	0.56	18	0.47	37	0.76	23
	Subadult	0.33	3	1.00	1	0.17	3	0.50	1
	Unknown	1.00	2	0	1	0	2		0
	Total	0.81	26	0.55	20	0.43	42	0.75	24

	Female	Females nesting		Nests successful		Fecundity		Productivity	
Year	Ageclass	Proportion	n	Proportion	n		n		n
1999	Adult	0.41	27	0.80	10	0.14	36	0.56	9
	Subadult	0	2		0	0	4		0
	Unknown		0		0	0	1		0
	Total	0.38	29	0.80	10	0.12	41	0.56	9
2000	Adult	0.77	30	0.82	22	0.50	33	0.87	19
	Subadult	0	1		0	0.50	3	0.75	2
	Unknown	1.00	1	0	1	0.33	3	1.00	1
	Total	0.75	32	0.78	23	0.49	39	0.86	22
2001	Adult	0.09	23	1.00	2	0.08	30	0.83	3
	Subadult	0.33	3	0	1	0	4		0
	Unknown	0	1		0	0	1		0
	Total	0.11	27	0.67	3	0.07	35	0.83	3
2002	Adult	0.97	32	0.89	28	0.79	33	0.93	28
	Subadult	0.67	6	1.00	3	0.50	7	1.17	3
	Unknown	1.00	1		0		0		0
	Total	0.92	39	0.90	31	0.74	40	0.95	31
2003	Adult	0.46	26	0.27	11	0.09	32	0.83	3
	Subadult	0.50	2	0	1	0.14	7	0.50	1
	Unknown	0	1		0	0	1		0
	Total	0.45	29	0.25	12	0.10	40	0.75	4
2004	Adult	0.70	33	0.90	21	0.55	32	0.92	18
	Subadult	0	1		0	0	1		0
	Unknown	1.00	2	1.00	2	0.50	3	0.75	2
	Total	0.69	36	0.91	23	0.53	36	0.90	20

Table 5. Nest tree and nest stand structural variables around California spotted owl nest trees in northeastern California, 1990-2000. After Blakesley et al (In Press 2005).

	Unique nests (n = 132)		Nest uses (n = 174)[a]	
Nest tree or nest stand attribute	Mean	CV	Mean	CV
Nest tree diameter at breast height (cm)	117	0.29	118	0.28
Percent slope above and below nest tree	25	0.55	27	0.48
Nest tree elevation (m)	1714	0.09	1701	0.08
Number of conifer stems/ha 13-40 cm dbh	140	0.92	156	0.92
Number of hardwood stems/ha 13-40 cm dbh	13	3.51	16	3.18
Percent canopy cover 10 meters from nest tree	82	0.14	83	0.13
Percent canopy cover 25 meters from nest tree	81	0.16	81	0.16
Log volume (m^3/ha)[b] of logs >25 cm diameter	25.25	0.74	26.08	0.69
Basal area (m^2/ha)[c] of trees >61 cm dbh	5.42	0.55	5.36	0.59
Basal area (m^2/ha)[c] of snags >61 cm dbh	1.17	1.00	1.38	0.95
	Summary			
Nest tree condition: live (L), snag (S)	L = 97, S = 35		L = 134, S = 40	
Nest type: platform (P), top cavity (T), side cavity (S)	P = 21, T = 45, S = 66		P = 22,T = 65, S = 87	
Nest tree species: fir (F), pine (P), other (O)	F = 63, P = 54, O = 15		F = 79, P = 83, O = 12	
Aspect of slope at nest tree: N, E, S, W	N = 45, E = 35, S = 22, W = 30		N = 59, E = 35, S = 31, W = 49	

[a] Many nests were used by owls in more than 1 year, yielding a greater sample size than the number of unique nests

[b] To convert m^3/ha to ft^3/acre, multiply by 87.3.

[c] To convert m^2/ha to ft^2/acre, multiply by 26.6.

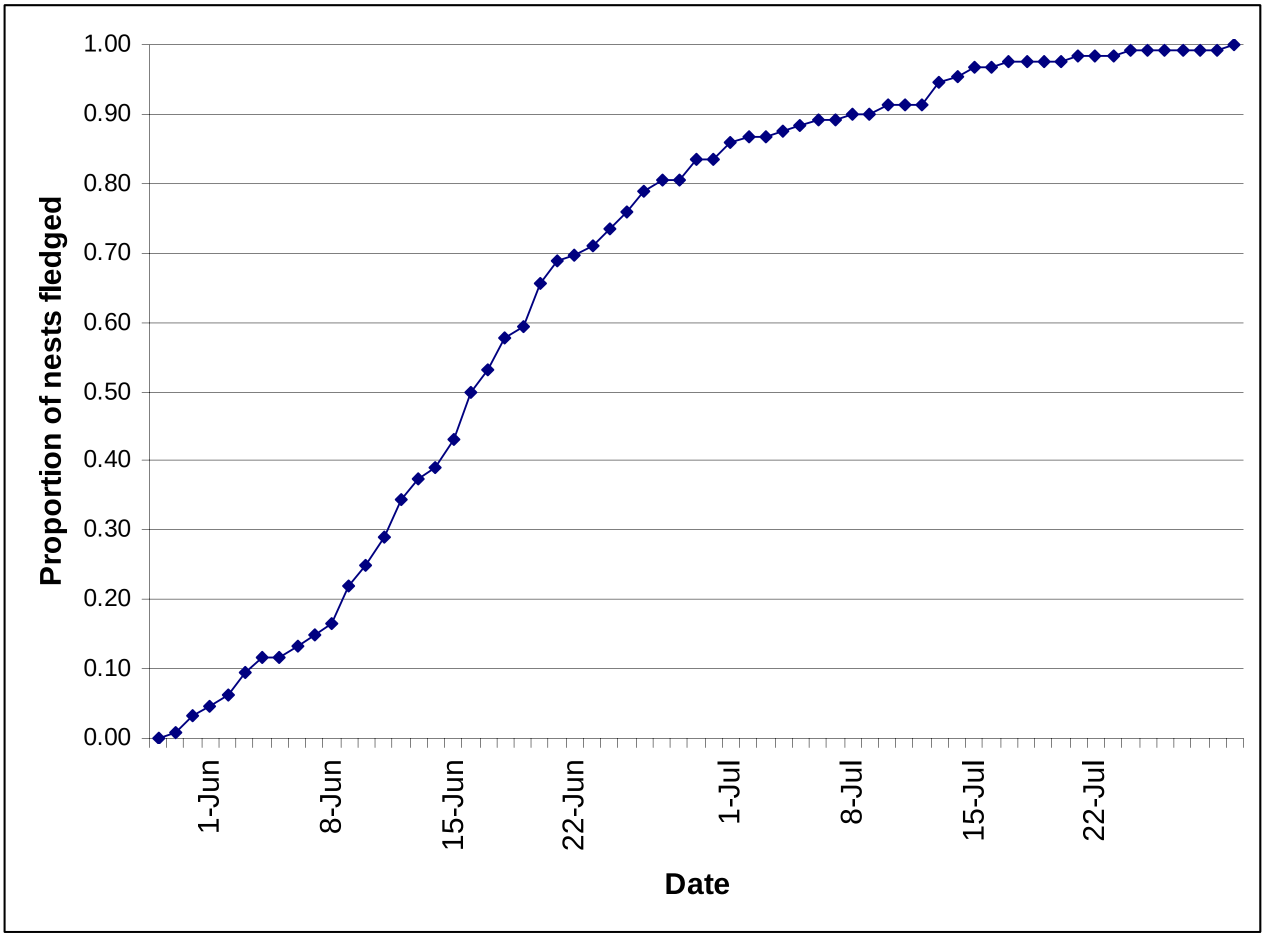

Figure 1. Cumulative distribution of California spotted owl fledging dates, 1990-2004 (*n* = 128 nests known to be active ≤21 days previous to the date fledglings were first observed).

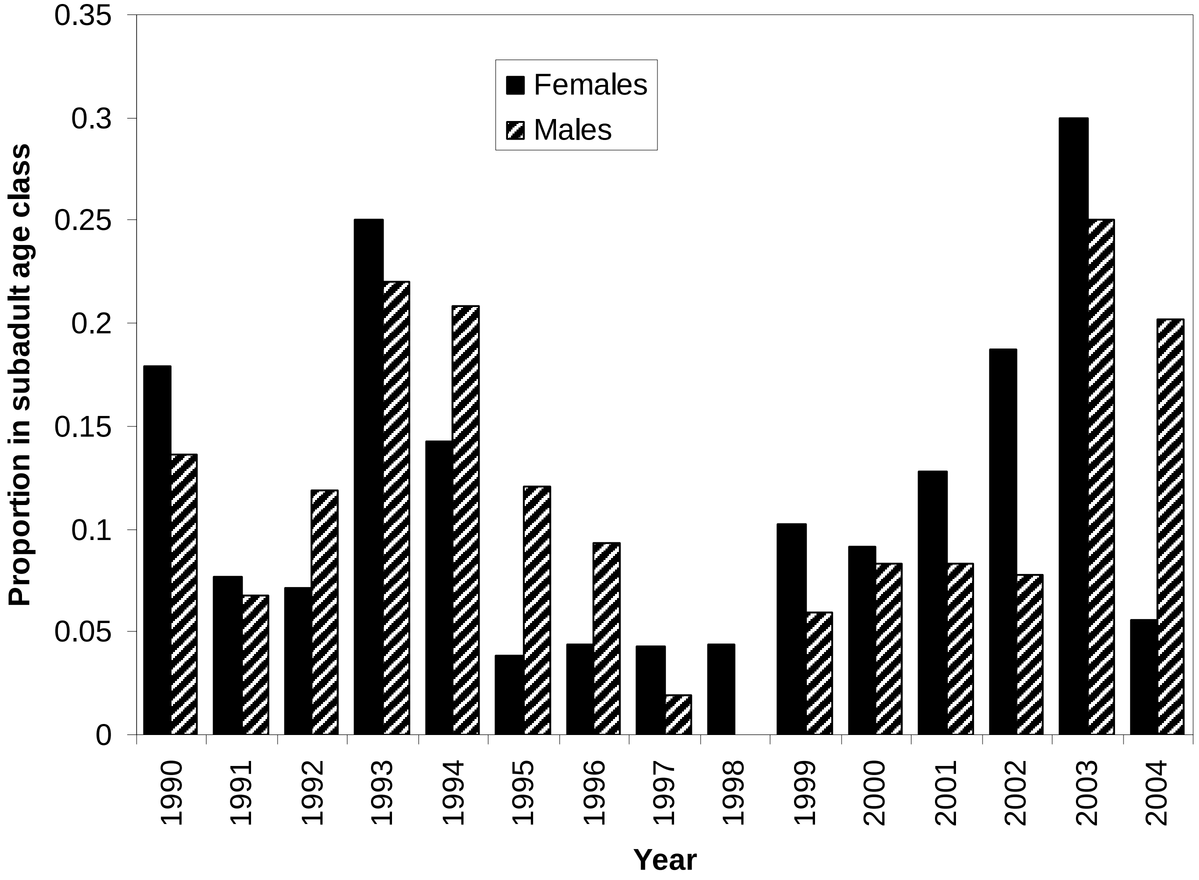

Figure 2. Proportion of California spotted owl population in the subadult age class (age < 3 years).

SITE OCCUPANCY, APPARENT SURVIVAL, AND REPRODUCTION OF CALIFORNIA SPOTTED OWLS IN RELATION TO FOREST STAND CHARACTERISTICS

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Abstract: The California spotted owl (*Strix occidentalis occidentalis*) has been at the center of political and administrative debate due to its association with commercially valuable forest. Several studies have compared the forest cover types used by California spotted owls with the cover types that are generally available, establishing the association between spotted owls and old/large tree components of forests at the landscape scale. We sought a deeper understanding of spotted owl habitat associations in areas in which owls had already selected territories. We mapped and classified vegetation within circular plots (radius 2.4 km) around 67 spotted owl sites in northeastern California, USA. We evaluated the relationships between habitat composition within the different owl sites and variation in (1) nest success (1990–2000) and (2) site occupancy, apparent survival probability, and reproductive output (1993–1998). All analyses included data representing 2 spatial scales: core area (814 ha) and nest area (203 ha). Site occupancy was positively associated with the amount of the nest area dominated by large trees with high canopy cover within the nest area. It was negatively associated with the amount of nonhabitat (nonforested areas and forest cover types not used for nesting or foraging) and with medium-sized trees with high canopy cover. Site occupancy also decreased with time and elevation. Apparent survival probability varied annually and was positively related to the area of each habitat class multiplied by the quotient proportion used/proportion available for each type, at both the nest and core scales. Reproductive output was negatively related to elevation and nonhabitat within the nest area. Nest success was positively associated with the presence of large remnant trees within the nest stand.

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Key words: California spotted owl, demography, forest cover types, habitat associations, nest success, reproduction, site occupancy, *Strix occidentalis occidentalis*, survival.

Administrative policy and political debate has centered on the California spotted owl due to its association with commercially valuable coniferous forest (U.S. Forest Service 1998, 2001, 2004; HFQLG 1998). The U.S. Forest Service sought to balance the demand for timber production in the Sierra Nevada with 2 other priorities: maintenance of habitat for spotted owls and forest carnivores, and reduction of the risk of catastrophic wildfire (U.S. Forest Service 2001, 2004). Despite years of effort devoted to preparing Sierra Nevada Forest Plan Amendments, debate continues regarding the forest conditions required by California spotted owls for survival and reproduction.

The California spotted owl inhabits coniferous and hardwood forests of the southern Cascades, western Sierra Nevada, and central and southern coastal mountains of California (Verner et al. 1992). Its association with old and large trees at the landscape scale is well established: several studies have shown that, throughout the Sierra Nevada, owls select forest stands that are dominated by large trees (>61-cm diameter at breast height [dbh]) and have moderate to high levels of canopy cover (≥40%), for foraging (Call et al. 1992, Zabel et al. 1992), nesting, and roosting (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, LaHaye et al. 1997, Moen and Gutiérrez 1997). In addition, owls used forest stands dominated by intermediate-sized trees (30–61-cm dbh) less than the availability of these stands in the landscape. At finer spatial scales, stands used by owls for roosting contained trees >100 cm dbh more frequently than did randomly selected stands (Moen and Gutiérrez 1997).

The studies cited above were important for discriminating the cover types used by owls from cover types generally available across the forest landscape. We sought a deeper understanding of spotted owl habitat associations by modeling spotted owl demographic response variables (site occupancy, apparent survival, reproductive output, and nest success) as a function of forest composition, predicated on owls having selected territories within the landscape. To evaluate these relationships, we used empirical data from

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a long term study of spotted owl demography (Blakesley et al. 2001, Franklin et al. 2004) in conjunction with vegetation maps and ground measurements taken in the immediate vicinity of spotted owl nests.

Our objectives were to determine (1) whether variability in site occupancy, apparent survival probability, or reproduction were related to attributes of forest cover and stand structure in territories of California spotted owls; (2) whether such relationships were stronger at the scale of home-range core areas or at the scale of smaller nest areas; (3) which characterization(s) of high-quality habitat best explained variation in site occupancy, apparent survival probability, and reproduction; and (4) whether forest cover type, nest tree characteristics, and/or local nest stand measures were related to nesting success.

STUDY AREA

Our study area encompassed 2,200 km^2 of the Lassen National Forest (LNF) and adjacent forested land in northeastern California, USA (40°00′–40°50′N, 120°30′–121°40′W). We studied 1 owl pair in Lassen Volcanic National Park, and several owls on private land managed primarily for timber production. Most forested stands on the study area were classified as white fir-mixed conifer, and were composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and red fir (*A. magnifica*). The study area is located at the southern end of the Cascade Geographic Province. However, it has been included in the Sierra Nevada Province for spotted owl management purposes (e.g., U.S. Forest Service 2001*a*), and it is near the northern limit of the distribution of the California spotted owl. Elevations on the study area ranged from 1,200 to 2,100 m.

Timber harvest in the Sierra Nevada has primarily been accomplished through selective thinning. Clearcut areas are uncommon in Sierra Nevada coniferous forests, in contrast to most forests in the range of the northern spotted owl. Forest cover is relatively continuous and there are few high-contrast edges at the landscape scale (Sierra Nevada Ecosystem Project 1996). Therefore, we did not attempt to quantify the spatial distribution of habitat, as was accomplished for 2 studies of northern spotted owl demography in relation to habitat (Franklin et al. 2000, Olson et al. 2004).

METHODS

Owl Data

We collected data on owls during an 11-year demographic study (Blakesley et al. 2001, Franklin et al. 2004), following a standardized field protocol similar to that used in studies of northern spotted owls (Franklin et al. 1996). The protocol was approved by the Colorado State University Animal Care and Use Committee. We located owls during night and daytime surveys and captured, banded, and resighted them to estimate apparent survival probability. Neither home range nor territory boundaries were known. However, because owls were individually identifiable with colored leg bands, we established the locations of owl sites by repeated observations of individuals and owl pairs at nest and roost locations (Hunsaker et al. 2002). We recorded occupancy data for each site in each year and categorized sites as pair, single, or unoccupied after 4 complete surveys of circular plots (2.4-km radius). We determined reproduction for as many sites as possible using standardized field procedures (Blakesley et al. 2001). We defined reproductive output as the number of offspring fledged at a site in a given year (0, 1, 2+), and we recorded zero for sites confirmed to be vacant or occupied by single males.

Vegetation Mapping

Vegetation was mapped within circular plots (2.4-km radius) centered on 67 spotted owl sites in and adjacent to the Almanor Ranger District of the Lassen National Forest. The area mapped contained approximately the western two-thirds of the owl territories in the study area. Homogeneous vegetation polygons were delineated and characterized using color aerial photographs, 2 sets of digital orthophoto quads (1993 and 1998) and timber sale information (Jo Ann Fites-Kaufmann, U.S. Forest Service, personal communication). Separate maps were created for each year from 1993 to 1998. The dominant tree size class, percent canopy cover and large tree density were estimated and assigned to 3-6 categories per variable for each polygon. We followed the standard size class and canopy cover categories used by the U.S. Forest Service for timber mapping (e.g., Verner et al. 1992) in order to make our results compatible with Forest Service methods, policies and land use planning. Size class categories were: zero (no trees), 1 (seedlings; <15-cm diameter at breast height [dbh]), 2 (small trees; 15–29-cm dbh), 3 (medium trees; 30–61-cm dbh), and 4 (large trees; >61-cm dbh). Canopy cover categories were zero (<10%), S (sparse; 10–25%), P (poor; 25–40%), N (normal; 40–70%), and G (good; >70%). Large tree density categories (number of trees >76-cm dbh per ha) were: zero (<1.2), 1 (1.2–4.9), 2 (4.9–14.8) and 3 (>14.8). Thus, a forest stand dominated by trees from 30 to 61-cm dbh with 50% canopy cover and 2 large trees per ha would be coded as 3N1.

We based our analyses on mapped vegetation polygons within circular plots with radii 0.8 and 1.6 km for 67 spotted owl sites. We selected 1 center for each site, defined by nest trees whenever possible ($n = 48$), and by areas of repeated roosting otherwise ($n = 19$). Specifically, selection of site centers followed this hierarchical process: we identified the Universal Transverse Mercator (UTM) coordinates of (1) the most frequently used nest; (2) if there was a tie, the most recently used nest; (3) if no nest was known, the most recent location of young juvenile owls; (4) if no juvenile location was known, the most recent pair roost location; and (5) if no pair was known, the most recent owl roost location. The coordinates of all nest trees were located with a Global Positioning System. Coordinates of roost locations were estimated in the field using 1:24,000 topographical maps and altimeters. We selected the larger plot size (814 ha; radius 1.6 km) based on the estimated size of spotted owl breeding season core areas in the LNF (Bingham and Noon 1996). Core areas were empirically estimated regions within the home range that received concentrated use. These core areas overlapped for several adjacent owl pairs, so we used approximately half the minimum distance between nest sites of adjacent pairs to define the radius of the smaller plot (0.8 km; area 203 ha), to represent the area assumed to be used exclusively by 1 pair, hereafter referred to as the nest area.

Combinations of the 3 vegetation measures resulted in 36 different polygon classifications within the core areas ($\bar{x} = 17$/site, range = 9–26). To reduce the number of explanatory variables in modeling site occupancy, apparent survival probability and reproductive output, we created habitat classes by grouping cover types based on current knowledge of spotted owl ecology (Table 1). We defined the category SELECT as cover types used by California spotted owls for nesting in greater proportions than were available in the landscape (Verner et al. 1992). We defined OTHER as cover types used for nesting by spotted owls proportionately less than available in the landscape (Verner et al. 1992). We created additional categories of SELECT and OTHER as areas with canopy cover >70% (CCG), presence of remnant trees (REM), or both (CCGREM; see Table 1). We calculated the variable NESTUSE by weighting all of the cover types used for nesting by the quotient proportion used/proportion available for each type (based on Verner et al. 1992). The final habitat class variable was NON, which represented the amount of nonforested land as well as forested stands not used by California spotted owls for nesting (dominated by small trees and/or low canopy cover; Verner et al. 1992).

We hypothesized that habitat classes selected by owls for nesting (SELECT, SELCCG, SELREM, SELCCGREM, NESTUSE) would be positively associated with spotted owl reproductive output and apparent survival probability. These competing variables may be considered alternative models of high-quality spotted owl habitat, and we designed our model sets to elucidate which characteristics of forest stands (dominant tree size, canopy cover, presence of large remnant trees) were most important for explaining variation in spotted owl demographic rates. We expected NON to be negatively

Table 1. Habitat classes used for modeling site occupancy, probability of apparent survival, and reproductive output of California spotted owls in northeastern California, USA.

Habitat class	Definition	Cover types
SELECT	Large trees with normal to good canopy cover	4N0 4N1 4N2 4G0 4G1 4G2 4G3
SELCCG	Canopy cover good	4G0 4G1 4G2 4G3
SELREM	Remnant trees present	4N1 4N2 4G1 4G2 4G3
SELCCGREM	Canopy cover good and remnant trees present	4G1 4G2 4G3
OTHER	Large trees with poor canopy cover; medium trees with poor to good canopy cover; small trees with good canopy cover	2G0 2G1 3P0 3P1 3P3 3N0 3N1 3N2 3G0 3G1 3G2 4P0 4P1 4P2
OTHCCG	Canopy cover good	2G0 2G1 3G0 3G1 3G2
OTHREM	Remnant trees present	2G1 3P1 3P3 3N1 3N2 3G1 3G2 4P1 4P2
OTHCCGREM	Canopy cover good and remnant trees present	2G1 3G1 3G2
NESTUSE	Medium and large cover types used for nesting, weighted by proportion used/proportion available.	0.65*(2G) + 0.29*(3P) + 1.19*(3N + 3G) + 0.48*(4P) + 2.26*(4N + 4G)
NON	Nonforested area or small trees	All size zero and 1; 2S 2P 2N 3S 4S

associated with spotted owl reproductive output and apparent survival probability.

We had no a priori basis for predicting the effects of habitat classes that were used by owls for nesting but not selected at the landscape scale (OTHER, OTHCCG, OTHREM, or OTHCCGREM) on either reproductive output or apparent survival probability. However, we hypothesized that selected habitat classes with canopy cover >70% and/or large remnant trees present (SELCCG, SELREM, or SELCCGREM) could exhibit stronger positive relationships with owl life history traits when combined with nonselected habitat classes having canopy cover >70% and/or large remnant trees present (SELCCG + OTHCCG, SELREM + OTHREM, or SELCCGREM + OTHCCGREM, respectively).

Nest Stand Measurements

We measured physiographic and vegetation characteristics immediately surrounding owl nest trees at 132 nests in 64 owl territories throughout the area of the demographic study. We established sampling strip plots 10 m in width, beginning 5 m from the nest tree and extending 30 m in each of the 4 cardinal directions. We measured dbh and height of all trees ≥40 cm dbh, all snags ≥12 cm dbh, and all logs ≥25 cm diameter within the entire plots. We measured dbh and height of trees <40 cm dbh in the central third of each plot and estimated canopy cover 10 m and 25 m from the nest tree in each of the 4 cardinal directions using a spherical densiometer. In addition, we recorded nest type (top cavity, side cavity, platform); species, dbh, and height of the nest tree; nest height; tree condition (live tree or snag); slope; aspect; and elevation. We used the vegetation polygon layer in a Geographic Information System (GIS) to determine the habitat class of stands containing owl nests.

Data Analysis

Site Occupancy.—We modeled site occupancy, *O*, as a function of habitat class in logistic regression with an ordered multinomial response: no owls (zero), single owl (1), owl pair (2), $n = 273$, using PROC LOGISTIC in the program SAS (SAS Institute 2000). As we had noticed a decline in site occupancy over time on the study area, we modeled year as a linear trend (T) as well as a categorical variable (t), and a constant (no year effect). In addition to the a priori models, we ran single habitat class covariate models containing SELCCG, SELREM and SELCCGREM, and a set of post hoc models that added the variable NON to the original models. We ran the habitat class models at 2 spatial scales (core and nest) in combinations with and without elevation, with and without T, and with and without NON, yielding 214 models.

We used Akaike's Information Criterion, corrected for small sample size (AIC_c), for model selection. Akaike weights, w_i, estimate the relative predictive strength of each model and may be viewed as the weight of evidence for model i (Burnham and Anderson 2002:75–77). Evidence ratios, w_i/w_k, express the relative likelihood of model i vs. model k (Anderson and Burnham 2002). Because the same variable may appear in several competing models, we estimated the relative importance of each variable by calculating the cumulative Akaike weights, $w_+(j)$, where $w_+(j)$ is the sum of w_i across all models in the set in which variable j occurred (Burnham and Anderson 2002:77–79).

For logistic regression, the maximum of $R^2 < 1$. Therefore, we measured the proportion of variance explained by a model using $\bar{R}^2$, the maximum-rescaled R^2, where $\bar{R}^2 = R^2/\max(R^2)$ (Nagelkerke 1991).

Apparent Survival.—We used a subset of the owl capture history data from the demographic study, which contained records of adult and subadult owls found at the 67 sites for which vegetation mapping was completed. For owls that moved between sites, we split capture histories so that the relevant portion of each history was associated with the corresponding vegetation data ($n = 231$ capture histories from 203 individual owls at 67 sites). For owls that moved from 1 site to another, we did not record "loss on capture" at the initial site. Consequently, our estimate of apparent survival probability, $\hat{\phi}$, was negatively biased. The purpose of our analysis, however, was to determine which habitat classes were positively or negatively associated with persistence at a site and not to estimate apparent survival probabilities per se. Thus, an owl's dispersal from a given site reflected negatively on the habitat class composition of that site.

We used the program RELEASE (Burnham et al. 1987:77) to evaluate goodness-of-fit of the data set to open population mark–recapture models. We used maximum likelihood methods, based on an a priori set of product-multinomial models (Lebreton et al. 1992) to estimate apparent survival probabilities. We modeled the effects of vegetation covariates on apparent survival probabilities using a linear model framework with logit link functions. We used program MARK (White and Burnham 1999) to obtain maximum likelihood estimates and AIC_c for model selection.

We initially modeled time and sex effects without habitat class covariates to determine the underlying structure of subsequent models. Only 1 set of habitat class covariates may be included per individual capture history; i.e., we could not incorporate changes in habitat over time in our analysis. Therefore, we used mean amounts of habitat classes at a site as the vector of habitat class covariates for all owls at that site. The candidate set of a priori models of apparent survival included time and sex effects and the habitat classes described above.

We estimated variance components using MARK (White and Burnham 1999) to assess how much process variance existed in the capture history data (Franklin et al. 2000). We ranked each owl site according to its overall reproductive output, and then grouped the sites into 7 ranked categories (n = 8–11 sites/group, 63 sites total) and estimated the apparent survival probability for owls in each group. This is similar to evaluating temporal variation, using "site quality" groups rather than year. The justification for these groupings was that a previous analysis indicated that fecundity and apparent survival probability were positively related on the Lassen study area (Blakesley 2003).

Reproduction.—We modeled reproduction, R, as a function of habitat classes using binomial logistic regression (no juveniles produced, including no breeding attempt and breeding failure [zero], 1–3 juveniles produced [1]), using PROC LOGISTIC in SAS (SAS Institute 2000). We used records for adult females only because subadult female spotted owls have much lower fecundity than do adult females (Blakesley et al. 2001). We used AIC$_c$ for model selection and estimated $\bar{R}^2$ for the best model. We included year in all models because of the high annual variability in reproduction in the population (Blakesley et al. 2001). After running all a priori models with year and habitat class covariates, we re-ran the models including elevation. In all cases, models with elevation had lower AIC$_c$ than models without elevation. Therefore, we eliminated all models without elevation.

Nest Success.—A large sample of nest tree and nest stand measurements was available from throughout the study area, with corresponding nest success data from 1990 to 2000 (n = 174 reproductive outcomes). Habitat class data were available for most of these records (n = 122 reproductive outcomes; 89 successes, 33 failures). Although other analyses were restricted to 1993–1998 because of limited availability of annual vegetation maps, we included all years in our analysis because nest stands were rarely affected by timber harvest between 1990–1993 and 1998–2000 (J. Blakesley, Colorado State University, personal observation). Nest stands that were harvested after the nest was used and before the area was mapped (n = 2) were eliminated from the data set.

We used logistic regression with PROC LOGISTIC in SAS (SAS Institute 2000) to model nest success, S, as a function of nest tree and nest stand characteristics, habitat class of the nest stand, and year, and we used QAIC$_c$ for model selection (AIC$_c$ corrected for overdispersion [lack of independence] in the data). We also created 3 variables for our analysis by breaking the cover type codes down into the variables SizeClass, CoverClass, and Remnant (binary). We hypothesized that nest success would be affected by the interaction between dominant size class and remnant trees within the nest stand, with remnants being more important in size class 3 than in size class 4 stands.

RESULTS

Landscape Composition

Seventy percent of the total mapped area, 78% of the owl core areas and 83% of nest areas were composed of forested stands dominated by trees ≥30 cm dbh (size class 3 or larger) with ≥40% canopy cover (codes N and G). The values of NESTUSE, SELECT, SELCCG, SELREM, SELCCGREM, and OTHCCG (3G0, 3G1, and 3G2) all increased as the scale of analysis around site centers decreased. In contrast, the percent composition of OTHER decreased with decreasing area around site centers (despite OTHCCG being higher). The following cover types each comprised <1% of the total mapped area: 3P1, 3P2, 3P3, 4P0, 4P1, 4P2, 3N2, 3G2, 4G3.

Variation in all cover types and habitat classes among sites was 14-126% greater within nest areas than within core areas. There was generally more variation among sites in the original cover types than in the aggregated habitat classes. For example, within nest areas, the coefficient of variation (CV) for cover types 4G0, 4G1, and 4G2-3 were 2.26, 1.47, and 1.75, respectively, whereas the CV for habitat class SELCCG (comprised of 4G0, 4G1, 4G2-3) was 0.88. Several habitat classes were strongly correlated with each other (Blakesley 2003); notably SELECT and OTHER (r = 0.90), NESTUSE and SELECT (r = 0.88), and NESTUSE and OTHER (r = –0.62).

Fifty-six percent of spotted owl nesting occurred in stands dominated by large trees (cover types 4G0, 4G1, 4G2, 4G3), even though these stands comprised only 16% of the mapped area (Fig. 1). No nests occurred in stands dominated by small trees (size classes 0, 1, 2), nor were any nests in stands dominated by medium or large trees with poor canopy cover (cover types 3S, 3P, 4S, 4P). Stands dominated by medium trees with normal canopy cover (cover types 3N0, 3N1, 3N2) comprised 24% of the mapped area, yet contained only 9% of all nesting attempts. Stands dominated by medium sized trees with good canopy cover and large remnant trees <1.2/ha (cover type 3G0) were used for nesting in proportion to availability within the mapped area (12%), whereas similar stands with remnant trees ≥1.2/ha (cover types 3G1 and 3G2) comprised 6% of the area and contained 14% of nesting attempts.

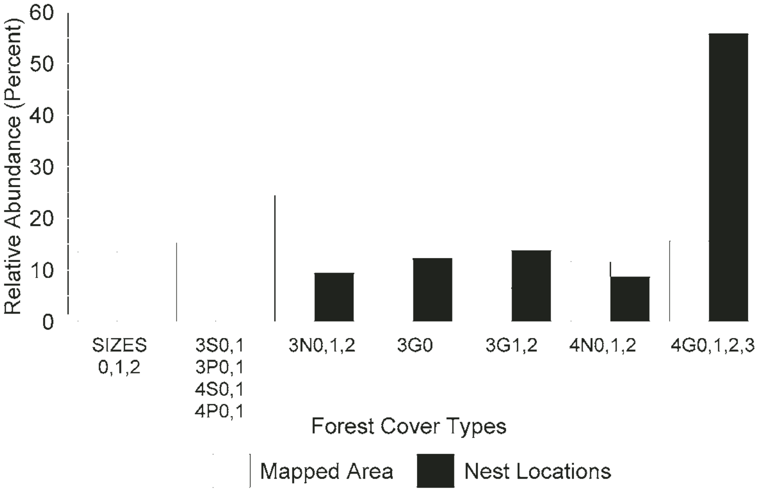

Fig. 1. Relative abundance (percent) of different cover types within circular plots (radius 2.4 km) around 67 California spotted owl site centers in northeastern California, USA, and relative abundance (percent) of nesting attempts (*n* = 138) within cover types. Cover type codes are described in text.

Only 4 of 92 nest trees (representing 5 of 138 nesting attempts) were <76 cm dbh, the size of remnant trees identified in air photos. However, 20 nest trees (representing 30 nesting attempts) were within stands classified as having <1.2 remnant trees/ha (cover types 3N0 and 3G0). Therefore, many of the large nest trees occurred at densities <1.2/ha within their respective forest stands.

Timber harvest occurred within 18 nest areas and 37 core areas from 1993 to 1997. Within sites subject to timber harvest, total harvest ranged from <1–60% of nest areas ($\bar{x}$ = 10%) and <1–48% of core areas ($\bar{x}$ = 4%).

Site Occupancy

All competitive models of site occupancy ($\Delta AIC_c < 5$) included a declining trend in occupancy over time (T); in the best model (lowest AIC_c), $\hat{\beta}$(T) = –0.33, SE ($\hat{\beta}$) = 0.10. When nest and core area models were considered together, the combined Akaike weight of core area models was <1% (Table 2). The best model revealed that the amount of nest area dominated by large trees and canopy cover >70% was positively associated with site occupancy ($\hat{\beta}$[SELCCG] = 0.0044, SE [$\hat{\beta}$] = 0.0019), whereas the amount of nest area dominated by medium-sized trees with canopy cover >70% and the amount of area unforested or dominated by small trees were negatively associated with site occupancy ($\hat{\beta}$[OTHCCG] = –0.0038, SE [$\hat{\beta}$] = 0.0015; $\hat{\beta}$ [NON] = –0.0094, SE [$\hat{\beta}$] = 0.0044). Adjusted R^2 of the highest ranked model = 0.18. Cumulative Akaike weights of all site occupancy models (Table 3) indicated that elevation was also an important explanatory variable and was negatively related to site occupancy (in the best model that included elevation, $\hat{\beta}$ [ELEV] = –0.00044, SE [$\hat{\beta}$] = 0.00033).

Apparent Survival

Results from program RELEASE indicated that the capture history data fit the assumptions of open population mark–recapture models. The structure of the data before adding covariates included an effect of year on apparent survival probability and an effect of sex on recapture probability (model ϕ [t] p [g]). The 4 top-ranked models indicated that apparent survival increased with greater amounts of habitat classes selected by the owls at the landscape scale and in stands dominated by large trees with normal to good canopy cover containing large remnant trees (best model: $\hat{\beta}$ [NESTUSE] = 0.242, SE [$\hat{\beta}$] = 0.141; best model containing SELREM: $\hat{\beta}$ [SELREM] = 0.242, SE [$\hat{\beta}$] = 0.141; Tables 3, 4). Although the remaining models with 1 habitat class covariate all explained more variation in apparent survival probability than did the model {ϕ (t) p (g)}, (i.e. they had lower deviance than the base model), the increase in number of parameters resulted in

Table 2. Models of site occupancy (O) including habitat class covariates for California spotted owls in northeastern California, USA, 1993–1998 (n = 273). Models are ordered by AIC_c. Habitat classes are defined in Table 1.

Model[a]	log(L)	K	AIC_c	ΔAIC_c	w_i
O (T + SELCCG + OTHCCG + NON)	–160.98	6	334.28	0.00	0.19
O (T + Elev + SELCCG + OTHCCG + NON)	–160.13	7	334.68	0.40	0.16
O (T + Elev + SELCCGREM + OTHCCGREM + NON)	–160.57	7	335.56	1.29	0.10
O (T + Elev + SELCCGREM + OTHCCGREM)	–161.74	6	335.79	1.52	0.09
O (T + SELCCG + OTHCCG)	–163.30	5	336.82	2.55	0.05
O (T + Elev + SELCCG + OTHCCG)	–162.44	6	337.19	2.91	0.05

[a] Models shown had Akaike weights (w_i) > 0.05 and were all for habitat classes within nest areas.

higher AIC_c values, and therefore we did not consider these models to be parsimonious.

The CV of process variation = 0.049, which suggests there was not much process variation to be explained by any variable. Reproductive rank for female owls (higher number = lower reproductive output) was related to apparent survival: $\hat{\beta}$ = –0.488, SE ($\hat{\beta}$) = 0.157.

Reproduction

Successful nests in 1993–1998 produced 1 or 2 fledglings with 1 exception: 1 nest produced 3 fledglings in 1998. Subadult (1- and 2-year-old) female spotted owls had lower reproductive rates than did adult females (Blakesley et al. 2001) and exhibited higher rates of breeding dispersal (Blakesley 2006). Because our sample size of subadult owls was small, we excluded subadults from analyses. Not all territories were sampled every year (n = 258 records from 63 mapped sites, 1993–1998).

Reproductive output varied by year, was lower at higher-elevation sites, and decreased as the amount of nest area that was unforested or dominated by small trees increased (best model: $\hat{\beta}$[ELEV] = –0.00078, SE [$\hat{\beta}$] = 0.00035; $\hat{\beta}$[NON] = –0.0080, SE [$\hat{\beta}$] = 0.0053; Tables 3, 5). Although many other models with habitat class covariates explained some variation in reproduction, they were less parsimonious than the second best model, which only contained year and elevation covariates.

Nest Stand Composition

Spotted owl nests occurred primarily in cavities of large live pines and firs (Table 6). Mean canopy cover in the immediate vicinity of the nest was virtually always >80%. Nest tree dbh ranged from 38–219 cm; however, 90% of nest trees were ≥76 cm dbh. The number of hardwood stems was highly variable because very few sites contained a measurable hardwood understory. Among the continuous nest site variables measured, the only strong correlation (>0.50) was between the 2 canopy cover measures (Blakesley 2003).

Nest Success

Nest success was higher when large remnant trees were present in the nest stand (best model: $\hat{\beta}$[REMNANT 0] = –0.826, SE [$\hat{\beta}$] = 0.247), and higher in size class 3 than size class 4 stands ($\hat{\beta}$[SIZE CLASS 3] = 0.636, SE [$\hat{\beta}$] = 0.266; Table 7).

Table 3. Cumulative Akaike weights (w+) of covariates in models of site occupancy, apparent survival probability, and reproductive output for California spotted owls in northeastern California, USA, 1993–1998 (n = 273). Habitat classes are defined in Table 1.

	Site occupancy		Apparent survival		Reproductive output	
Covariate[a]	w_+	sign of $\hat{\beta}$	w_+	sign of $\hat{\beta}$	w_+	sign of $\hat{\beta}$
SELECT	0.10	Positive	0.11	Positive	0.28	Positive
SELCCG	0.55	Positive	0.10	Positive	–	–
SELREM	–	–	0.17	Positive	0.13	Positive
SELCCGREM	0.31	Positive	0.12	Positive	–	–
OTHER	–	–	0.06	Negative	–	–
OTHCCG	0.50	Negative	–	–	–	–
OTHCCGREM	0.32	Negative	–	–	–	–
NESTUSE	–	–	0.24	Positive	0.23	Positive
NON	0.67	Negative	0.08	Negative	0.47	Negative
Elevation	0.58	Negative	0.04	Negative	0.46	Negative
Year	–	–	1.00	–	–	–
T (time trend)	0.99	Negative	–	–	–	–

[a] Covariates with Akaike weights ($w+$) < 0.05 are not shown.

Table 4. Models of apparent survival probability (ϕ) including habitat class covariates for California spotted owls in northeastern California, USA, 1993–1999 (n = 136). All models included effects of sex on probability of recapture. Models are ordered by AIC_c. Habitat classes are defined in Table 1.

Model [a]	Area	log(L)	K	AIC_c	ΔAIC_c	w_i
ϕ (Year + NESTUSE)	Nest	–196.22	9	411.00	0.00	0.13
ϕ (Year + NESTUSE)	Core	–196.46	9	411.48	0.48	0.10
ϕ (Year + SELREM)	Nest	–196.68	9	411.93	0.93	0.08
ϕ (Year + SELREM)	Core	–196.68	9	411.93	0.93	0.08
ϕ (Year)		–197.75	8	411.95	0.95	0.08
ϕ (Year + SELCCGREM)	Core	–197.03	9	412.63	1.62	0.06
ϕ (Year + SELCCGREM)	Nest	–197.03	9	412.63	1.63	0.06
ϕ (Year + SELCCG)	Core	–197.06	9	412.69	1.69	0.06
ϕ (Year + SELECT)	Core	–197.07	9	412.71	1.71	0.06
ϕ (Year + SELECT)	Nest	–197.15	9	412.88	1.88	0.05
ϕ (Year + SELCCG)	Nest	–197.24	9	413.06	2.06	0.05
ϕ (Year + NON)	Nest	–197.29	9	413.15	2.15	0.05

[a] Models shown had Akaike weights (w_i) > 0.05.

Table 5. Models of annual reproductive output (R) of California spotted owls in northeastern California, USA, 1993–1998 (n = 258). Models are ordered by AIC_c. Adjusted R^2 of the highest ranked model = 0.25. Models shown had Akaike weights (w_i) >0.05.

Model [a]	Area	log(L)	K	AIC_c	ΔAIC_c	w_i
R (Year + Elev + NON)	Nest	–114.55	8	245.67	0.00	0.11
R (Year + Elev)		–115.74	7	245.93	0.26	0.09
R (Year + Elev + NESTUSE)	Nest	–115.27	8	247.13	1.46	0.05
R (Year + Elev + SELREM)	Nest	–115.39	8	247.37	1.70	0.05

[a] Habitat classes are defined in Table 1.

Table 6. Nest tree and nest stand structural variables around California spotted owl nest trees in northeastern California, USA, 1990–2000.

		Unique nests (n = 132)		Nest uses (n = 174)[a]	
Code	Definition	Mean	CV	Mean	CV
DBH	Nest tree diameter at breast height (cm)	117	0.29	118	0.28
Slope	Percent slope above and below nest tree	25	0.55	27	0.48
Elev	Nest tree elevation (m)	1,714	0.09	1,701	0.08
SmallCon	Number of conifer stems/ha 13–40 cm dbh	140	0.92	156	0.92
SmallHw	Number of hardwood stems/ha 13–40 cm dbh	13	3.51	16	3.18
Cancov10	Percent canopy cover 10 meters from nest tree	82	0.14	83	0.13
Cancov25	Percent canopy cover 25 meters from nest tree	81	0.16	81	0.16
LogVol	Log volume (m^3/ha) of logs >25 cm diameter	25	0.74	26	0.69
LiveBasal	Basal area (m^2/ha)/acre of trees >61 cm dbh	5.4	0.55	5.4	0.59
SnagBasal	Basal area (m^2/ha)/acre of snags >61 cm dbh	1.2	1.00	1.4	0.95
			Summary		
TreeCond	Nest tree condition: live (L), snag (S)	L = 97, S = 35		L = 134, S = 40	
NestType	Nest type: platform (P), top cavity (T), side cavity (S)	P = 21, T = 45, S = 66		P = 22,T = 65, S = 87	
Species	Nest tree species: fir (F), pine (P), other (O)	F = 63, P = 54, O = 15		F = 79, P = 83, O = 12	
Aspect	Aspect of slope at nest tree: N, E, S, W	N = 45, E = 35, S = 22, W = 30		N = 59, E = 35, S = 31, W = 49	

[a] Many nests were used by owls in more than 1 year, yielding a greater sample size than the number of unique nests.

Table 7. Models of nest success (S) including habitat class, nest tree, and nest stand structural covariates for California spotted owls in northeastern California, USA, 1990–2000 (n = 122). Models are ordered by $QAIC_c$. Adjusted R^2 of the highest ranked model = 0.16. Models shown had Akaike weights (w_i) > 0.05. Variables are defined in Table 6.

Model	log(L)	K	AIC_c	ΔAIC_c	w_i
S (Remnant + SizeClass)	–64.29	4	112.46	0.00	0.60
S (Remnant + SizeClass + Remnant * SizeClass)	–64.26	5	114.58	2.12	0.21
S (Remnant)	–67.49	3	115.50	3.04	0.07
S (CoverType)	–63.23	7	122.00	4.55	0.06

DISCUSSION

Although owls were found nesting and roosting in a variety of forest stand types, site occupancy and apparent survival increased with increasing amounts of habitat classes known to be selected by the owl at the landscape scale. Reproductive output decreased as the amount of nonhabitat within the nest area increased. Nest success was higher where remnant trees were present and higher in stands dominated by medium-sized trees than by large trees. The relationships of habitat class variables to demographic response variables consistently occurred as hypothesized, except that fewer owls occupied areas dominated by medium sized trees with high canopy cover than we expected. The composition of habitat in the nest area (203 ha) was a much better predictor of site occupancy than was the composition of habitat in the core area (814 ha), but relationships between habitat variables and apparent survival and reproductive output were similar at both spatial scales. Our models also revealed a decline in site occupancy over time and showed yearly variation in apparent survival probability. Site occupancy, reproductive output, and, to a lesser extent, apparent survival declined with increasing elevation.

The relatively low variability in habitat classes among nest and core areas within the study area limited the power of forest composition data to explain variation in demographic data. In addition, some variation among sites was lost when the original polygon classifications (cover types) were aggregated into habitat classes. Furthermore, the strong correlations between habitat classes limited the predictive power of models containing more than 1 habitat class variable.

Our use of broad categories of canopy cover and dominant tree size class may have limited our ability to draw stronger inferences from the data. "Normal" canopy cover in our study was defined as 40–70%, masking our ability to evaluate differences in response variables within this range of canopy cover. Similarly, stands dominated by all trees >61 cm dbh were classified as size class 4. This is roughly half the mean size of trees used for nesting (117-cm dbh); a larger size class category may be more strongly associated with spotted owl site occupancy, survival or reproduction. Furthermore, in 16 cases (within 3N0 and 3G0), remnant classification failed to account for the nest tree; we recommend mapping remnant trees at densities lower than 1.2/ha in size class 3 stands.

Some of the observed variation in reproduction among territories may have been due to individual differences in ability to produce eggs or care for young. Because spotted owls are long lived and have strong site fidelity (Blakesley 2006), our data set is insufficient to separate the effects of site quality and individual owl quality on reproduction and survival. In magpies (*Pica pica*), individuals change territories and/or mates between years frequently enough for researchers to compare the effects of territory quality and bird quality on breeding success (Goodburn 1991). In one study, female quality accounted for 60% of the variance in magpie clutch size and male quality accounted for 70% of annual nesting success (Goodburn 1991).

The positive association we found between habitat classes affecting survival and fecundity contrasts with the trade-off found for northern spotted owls in northwestern California, in which the amount of interior mature and old-growth forest was positively associated with survival and negatively associated with reproductive output (Franklin et al. 2000). Both survival and reproductive output were positively associated with the length of edge between mature/old-growth forest and other vegetation types, including younger forest (Franklin et al. 2000). As a partial explanation of this pattern, Franklin et al. (2000) noted that dusky-footed woodrats (*Neotoma fuscipes*) are the primary prey of northern spotted owls in northwestern California (Ward et al. 1998) and are found in highest densities in sapling/brushy pole timber stands <25-years-old (Sakai and Noon 1993). Ecotones between mature/old forest and early seral forest may provide areas where woodrats are abundant and accessible to spotted owls (Franklin et al. 2000).

Olson et al. (2004) found that a mixture of older forest with younger forest and nonforested areas appeared to benefit northern spotted owl survival in the Oregon Coast Range. Habitat explained a negligible amount of variation in northern spotted owl reproduction in the Oregon Coast Range (Olson et al. 2004), where woodrats and flying squirrels (*Glaucomys sabrinus*) each comprised 37–39% of spotted owl prey (Forsman et al. 2004).

Previous research found that the primary prey of California spotted owls on the Lassen study area was northern flying squirrels (61% of the diet; Verner et al. 1992). Flying squirrel densities in the Lassen study area were highest in old forest stands, lowest in shelterwood logged stands, and intermediate in young forest stands (Waters and Zabel 1995). Although the interspersion of young and old forest stands appeared to benefit spotted owl reproduction in northwestern California where dusky-footed woodrats dominated the owls' diet, the presence of young forest stands did not appear to benefit spotted owl reproduction in this study, where flying squirrels dominated the diet.

The decline in site occupancy over time that we identified corroborates evidence from other analyses of these spotted owl demographic data, in which the spotted owl population declined during the study period (Blakesley et al. 2001, Franklin et al. 2004).

MANAGEMENT IMPLICATIONS

Site occupancy and apparent survival of California spotted owls were enhanced in habitats with features known to be selected by the owl at the landscape scale. Land managers in the Sierra Nevada region should retain forest stands dominated by large trees with canopy cover >70% and minimize the amount of area unsuitable to spotted owls within 200 ha surrounding spotted owl site centers to promote site occupancy and increase spotted owl reproductive output. Our results suggest that within owl core areas (814 ha), increases in the availability of habitat used by spotted owls for nesting, roosting and foraging will increase owl survival. Large remnant trees >76 cm dbh should be retained in all forest stand types that are used by spotted owls for nesting or managed as potential future spotted owl nesting habitat.

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Space use, forays, and habitat selection by California Spotted Owls (*Strix occidentalis occidentalis*) during the breeding season: New insights from high resolution GPS tracking

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ABSTRACT

Our current understanding of the relationship between imperiled species and forest management can benefit from global positioning system (GPS) technologies. Fauna of lateseral stage forests have historically been difficult to detect and track in rugged terrain, leading to challenges in movement characterization and conservation. We investigated movement of California Spotted Owls (*Strix occidentalis occidentalis*) using automated GPS loggers affixed to 15 owls in the northern Sierra Nevada, California. We used > 17,000 locations from individual owls to characterize homerange size, movement distances, and roosting and foraging habitat selection at four spatio-temporal scales (landscape, home range, foray, nightly) during the breeding season (April–August). Additionally, we assessed owl use of Protected Activity Centers (PACs), which are designated by the U.S.D.A. Forest Service to protect nesting and roosting habitat. Our results corroborated some previous findings about habitat requirements of California Spotted Owls, while also revealing new nuances in space use and habitat selection. Roosting and foraging owls selected stands with high canopy cover and large trees at multiple spatio-temporal scales, with foraging owls showing strongest selection at the largest (landscape) scale investigated. Although owls selected for PACs while foraging and roosting, PACs protected less than one quarter of foraging space use (volume of use) and fewer than half of observed roosts during the breeding season. Female owl home ranges were double the size of male home ranges, and distances travelled from the nest by females were 1.3 times greater than distances travelled by males, with non-breeding females travelling farthest and visiting up to six PACs during a single breeding season. Foraying behavior of this sort has not been documented previously in California Spotted Owls. Our findings support protection of later seral stage forest attributes for roosting and foraging California Spotted Owls. Given their selection for later seral forest attributes, strongest evidence of foraging habitat selection at the landscape scale, long distances travelled by owls and limited habitat protection afforded by PACs, habitat connectivity across the landscape is likely an important component for owl conservation, and distribution of current protected areas may be inadequate for this wide-ranging species.

1. Introduction

Spotted Owls (*Strix occidentalis*) are threatened by loss and fragmentation of later seral forest and invasion by congeneric Barred Owls (*Strix varia*), which displace and hybridize with Spotted Owls (Keane, 2017). Consequently, Spotted Owls have been a focus of forest conservation efforts in the western U.S. since the 1980s (Simberloff, 1987) and a primary factor in the development of some of the country's largest and most comprehensive management plans, including the Northwest Forest Plan which addressed management of 9.9 million ha in 3 states (Tuchmann et al., 1996). While the Northern Spotted Owl (*S. o. caurina*) and Mexican Spotted Owl (*S. o. lucida*) subspecies are

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federally protected, the California Spotted Owl (*S. o. occidentalis*) is currently under review for listing (U.S. Fish and Wildlife Service, 2017). The U.S.D.A. Forest Service, which manages lands where the majority of the California subspecies occurs, is currently reviewing a draft conservation strategy for the subspecies. While the California Spotted Owl is a high-profile and well-studied species, few of the management recommendations developed and implemented to protect it have been tested empirically (Berigan et al., 2012), and numerous questions remain on the most effective strategy to prevent its extinction (Stine and Manley, 2017).

California Spotted Owls are medium-sized owls that specialize in later seral stage forests (stands with high canopy cover and large trees) in montane regions of California (Tempel et al., 2016; Moen and Gutiérrez, 1997). They are socially monogamous central place foragers that defend territories around their nests, where they hunt at night and prey upon small mammals, birds, lizards and insects (Gutiérrez et al., 2017). Previous investigations established that spotted owls preferentially roost and nest in mature forest stands with later seral or old-growth characteristics (Moen and Gutiérrez, 1997; Bond et al., 2004; Tempel et al., 2016; North et al., 2017). Within mature forests, California Spotted Owls forage within a variety of habitats including stands with moderate to high canopy cover (Call et al., 1992; Williams et al., 2011), forest edges (Eyes et al., 2017; Williams et al., 2011), unlogged burned areas (Bond et al., 2016, 2009), and riparian corridors (Bond et al., 2016; Irwin et al., 2007).

Historically, conservation of California Spotted Owls has focused on protecting nesting and roosting habitat in later seral forests with high canopy cover and prevalence of large trees (Bond et al., 2004; Moen and Gutiérrez, 1997; North et al., 2017; Tempel et al., 2016). Habitat protection on National Forest lands generally occurs at the scale of "Protected Activity Centers" (PACs), where contiguous habitats are designated to protect core breeding and roosting behaviors for known pairs or territorial but unpaired owls (Berigan et al., 2012; U.S.D.A. Forest Service, 2004). Protected Activity Centers were proposed as part of an interim conservation strategy for the California Spotted Owl in 1992 (Verner et al., 1992b) to protect areas where owl use is concentrated within the home range, including nest and roost sites (Berigan et al., 2012). In practice, PACs are delineated as ≥121 ha polygons encompassing the best quality habitat (large trees and high canopy cover) around a California Spotted Owl nest or roost site. Stand-altering activities, except for chainsaw thinning small diameter material (< 15 cm diameter at breast height) and light under-burning, are generally prohibited within the PACs (Berigan et al., 2012). However, foraging California Spotted Owls in the Sierra Nevada utilize much broader areas than those encompassed by PACs, with individual owl home range estimates during the breeding season ranging from 500 to 2800 ha and year-round home range estimates exceeding 5000 ha (Williams et al., 2011; Zabel et al., 1992).

Habitat selection is dependent on spatial and temporal scales (Mayor et al., 2009; Orians and Wittemberg, 1991). For example, Blakesley et al. (2005) found that finer scale habitat features were better predictors of breeding site occupancy of California Spotted Owls, whereas LaHaye et al. (1997) reported that landscape scale features were better predictors of nest success. For foraging owls, Bond et al. (2016) found that the strength and direction of selection of burned habitat by owls was influenced by area designated as available habitat. Past assessments of habitat selection and space use by California Spotted Owls at multiple scales, and therefore evaluations of the efficacy of management, have been limited by available survey methods. For example, current knowledge of California Spotted Owl foraging behavior is based on auditory, and very high frequency (VHF) radio telemetry surveys, both of which are inherently biased toward areas that are more accessible to observers and are limited in spatial accuracy (Tomkiewicz et al., 2010).

Recent advances in animal tracking using Global Positioning Systems (GPS) and launch of the ICARUS satellite tracking program permit collection of increasingly precise, detailed, and extensive data on movement and locations of highly mobile and cryptic species (Tomkiewicz et al., 2010; Wikelski, 2007). These technological developments have the potential to provide insights that will greatly improve our understanding of animal-habitat relationships and inform conservation planning (Morales-Reyes et al., 2017; Shimada et al., 2017). Forest-dwelling fauna have historically been difficult to detect and track in rugged terrain (Hollenbeck et al., 2018; Phoebus et al., 2017). This limitation has constrained the scope of research questions addressed, leading to a focus on conservation of habitat components in which species can be readily detected, and a neglect of life-history phases in areas where study subjects are more difficult to detect (Koenig et al., 1996). For example, movements and activities of central place foragers during nesting are a major research and conservation focus, but relatively little is known about movements of central place foragers during forays and dispersal (Clobert et al., 2012; Kesler and Walters, 2012; Rosenberg and McKelvey, 1999). Detailed information from high resolution GPS tracking can provide more robust support for existing forest management strategies, which are rarely empirically tested, or spur development of more refined and ecologically relevant approaches.

Our objective was to revisit current knowledge of California Spotted Owl habitat selection and space use by investigating movement of California Spotted Owls using GPS loggers that automate observations of movements at multiple temporal and spatial scales (Wilmers et al., 2015). Throughout three breeding seasons (April –August 2015–2017), we characterized California Spotted Owl homerange size, transit distances and straight-line distances from the nest, selection of roosting habitat, and selection of foraging habitat at four spatio-temporal scales. We used a model selection approach to evaluate whether owls selected for specific habitats and whether sex or breeding status influenced homerange, movement distance from the nest or habitat selection. We also assessed the proportion of each owl's observed roost sites and foraging volume of use within designated PACs and evaluated selection for these protected areas.

2. Materials and methods

2.1. Study area

We studied California Spotted Owls on the Mt. Hough Ranger District, Plumas National Forest (63,770 ha), within the Sierra Nevada mountain range in northern California (40°00′01″N 120°40′05″W, Fig. 1). The Forest has an elevation gradient of 311 to 2433 m and a Mediterranean and montane climate with dry, warm summers and cool, wet winters. Although conditions vary widely across the elevation gradient, mean annual precipitation within the Forest is c. 1036 mm, and mean temperature ranges from 1.3 ± 2.4 °C in January to 19.3 ± 1.5 °C in July (1895–2017, Western Regional Climate Center, 2017). Vegetation in Plumas National Forest is dominated by lower and upper montane forest with stands of ponderosa pine (*Pinus ponderosa)* – mixed conifer, white fir (*Abies concolor*) – mixed conifer, and red fir (*Abies magnifica*) (Fites-Kaufman et al., 2007). Common tree species include red fir, white fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine, Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), black oak (*Quercus kelloggii*) and incense cedar (*Calocedrus decurrens*) (Fites-Kaufman et al., 2007). Fire is common throughout the region and mixed-severity fire regimes dominate, with tree scar records indicating composite fire return intervals on the forest ranging from 8 to 22 years at a site between 1454 and 2001 (Moody et al., 2006).

2.2. Owl movement surveys

During 2015–2017 we marked and tracked 8 females and 7 males from 8 territories and collected a mean of 805 (370–1072) locations per owl*season during 22 owl*seasons (15 individual owls were tracked, 5

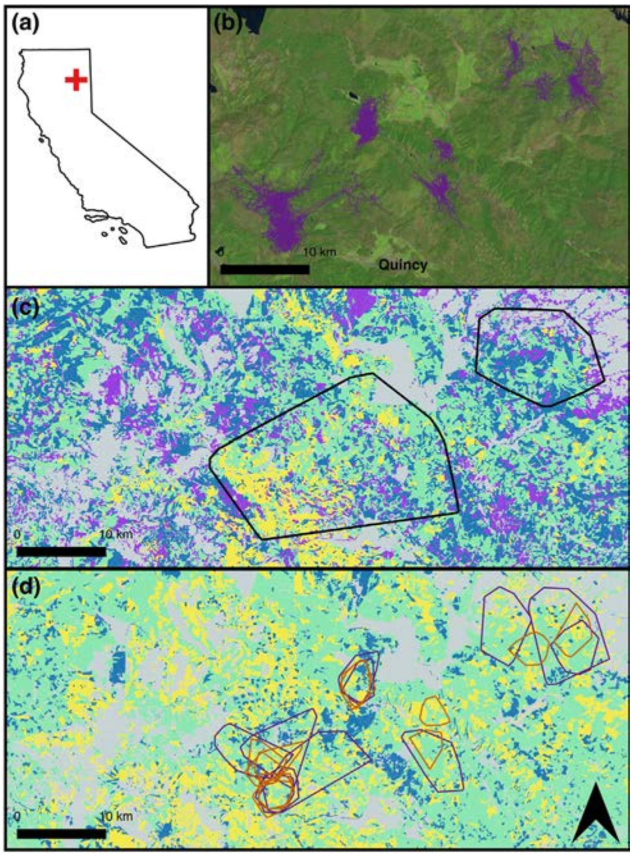

Fig. 1. Study area (a) in Plumas National Forest, California; (b) trajectories (purple traces) of 15 California Spotted Owls tracked during the 2015–2017 breeding seasons (April–August); (c) minimum convex polygons (MCPs) of all owl locations in east and west landscapes within the study area and overlaid on canopy cover (> 70% is yellow, 50–70% is green, 30–50% is blue, and < 30% is purple); (d) home ranges defined by MCPs for male (orange, 11 owl*seasons) and female (purple, 11 owl*seasons) in each season and overlaid on dominant tree size (DBH > 50 cm is yellow, 25–50 cm is green, < 25 cm is blue). Grey background in (c) and (d) show treeless areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of them during multiple breeding seasons) across > 45,000 ha of forest (Supplementary material, Appendix S1). We used Forest Service data on known nests coupled with surveys to locate owls in May and June of 2015, 2016, and 2017. We captured owls by hand and with snare and noose poles. Owls were tagged under authorization from the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645) and the U.S.F.W.S. Bird Banding Laboratory (Permit #22423). We determined owl sex based on pitch of vocalizations or knowledge from prior banding efforts, and we classified owl age using plumage characteristics (Forsman, 1983; Franklin et al., 1996). When tracking began, one female owl was in its second year (SY, F) and 14 owls were after third year (ATY, 7F:7M). We attached an Alle-300 GPS-UHF GPS logger (Ecotone Telemetry, Sopot, Poland) and a VHF transmitter (Advanced Telemetry Systems, Isanti, U.S.A.) to each bird using a back-mounted Teflon ribbon harness (total package weight < 13 g) (n = 15, seven males and eight females). The GPS-UHF units recorded locations at defined intervals within daily duty cycles, and stored locations until a connection was established with a hand-held or stationary base station to which locations were then transmitted (EP-BS, Ecotone Telemetry). We placed base stations near nests or in areas commonly transited by owls. Additionally, owls were tracked on foot to within 50–200 m using VHF radio telemetry and data were downloaded from the GPS-UHF units using a wireless link to the base station.

These GPS-UHF units can be remotely reprogrammed, enabling use of multiple sampling regimes over time on individual owls. During the breeding season, batteries on the GPS-UHF units allowed approximately 3 months of tracking after marking (c. 10 May), with hourly locations collected daily between c. 1800 h and 600 h the following day. We also programmed GPS-UHF units to collect 3–7 nights of higher-resolution movement data for each owl, with locations collected at 1–6 min intervals. Herein, we truncated movement data to align with the California Spotted Owl breeding season from 1 April–31 August (Garcia-Feced et al., 2011; Lee et al., 2012; Tempel and Gutiérrez, 2013). Foraging location observations were defined as position coordinates recorded between 1 h after sunset and 1 h before sunrise. We defined roost locations as locations recorded between 2 h after sunrise and 2 h before sunset. We determined the breeding status (breeding or non-breeding) of owls during each season through survey efforts or direct observation.

2.3. Homerange size

We calculated homerange size using the minimum convex polygon (MCP) method (Worton, 1987), so that our calculations would be comparable to the majority of literature on California Spotted Owl home range (see Roberts, 2017 and references therein). MCPs were derived for each owl*season using all available locations. For robustness, we also calculated home ranges using the 95% isopleth of the kernel density utilization distribution (Worton, 1989). We compared homerange size between sexes and breeding status classes using a model selection process to test specific hypotheses about homerange size (Table 1). We used an information-theoretic approach to model selection (Burnham and Anderson, 2003) and evaluated support for 4 hypotheses related to homerange size (Table 1). For each dataset, we compared candidate models using the Akaike information criterion, adjusted for sample size (AIC_c), and retained the best approximating model with the lowest AIC_c value, or the best set of models, if top models were within 2 ΔAIC_c (Burnham and Anderson, 2003). As a final step, we assessed the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and evaluating whether it significantly improved model fit (reduced $AIC_c > 2$). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Models were fit using log-transformed homerange size (ha) as the response variable, to satisfy the assumption of normality. We included *territory* as a random effect only (not individual) because a parametric bootstrap test showed that when *individual* was added to the final model it was not significantly different from the model containing only *territory* (LRT = 74.22, P = 0.500). We conducted all analysis within the R environment for statistical computing (R Development Core Team, 2016). We used the *adehabitatHR v3.3.0* (Calenge, 2006) package to fit MCPs and kernel density utilization distrubtions, packages *lme4 v1.1-12* (Bates et al., 2013) and *lmerTest v 2.0-33* (Kuznetsova et al., 2017) to fit linear mixed effects models and *MuMIn v 1.40.4* was used for model averaging and to calculate R^2 of all models using methods described in Nakagawa and Schielzeth (2013). We considered differences significant at $\alpha < 0.05$, and we report test statistics (TS) and 95% confidence intervals (95% CI) where appropriate; test statistics were t values for single models and z values for model-averaged sets.

2.4. Distance travelled

We calculated nightly distance transited (sum of all nightly movements) using only high resolution data (1–6 min position interval) for full nights (> 6 h data collection). We also calculated maximum distance travelled from the nest (straight-line distance) for each owl*-season and each night. We defined nest locations as active nests for breeding birds and nest site from prior year for non-breeding birds, due

Table 1

Hypotheses and corresponding models developed to explain variation in California Spotted Owl homerange size and distance travelled from nest during breeding seasons of 2015–2017. Homerange size (ha) was defined by MCP for each owl*season and models were linear mixed effects models with territory included as a random effect. Distance travelled from nest was the maximum straight-line distance from the nest for each night and models were Gaussian mixed effects models with a log-link and with individual owl included as a random effect. Nest locations represented active nests for breeding birds and nest sites during prior years for non-breeding birds.

Hypothesis	Model equation
Homerange size	
1. Owl homerange size was not influenced by sex or breeding status	Homerange size $\sim\beta_0$ + (1|territory)
2. Home range size differed between males and females	Homerange size $\sim\beta_0 + \beta_1$*sex + (1|territory)
3. Home range size differed between non-breeding and breeding birds	Homerange size $\sim\beta_0 + \beta_1$*breeding_status + (1|territory)
4. Sex and breeding status influenced homerange size	Homerange size $\sim\beta_0 + \beta_1$*sex + β_2*breeding_status (1|territory)
Distance travelled from nest	
1. Nightly maximum distance from the nest was not influenced by sex or breeding status.	Distance from nest $\sim\beta_0$ + (1|individual)
2. Distance travelled from nest differed between sexes	Distance from nest $\sim\beta_0 + \beta_1$*sex + (1|individual)
3. Distances travelled from nest differed between breeding and nonbreeding birds	Distance from nest $\sim\beta_0 + \beta_1$*breeding_status + (1|individual)
4. Sex and breeding status influenced distances travelled from the nest	Distance from nest $\sim\beta_0 + \beta_1$*sex + $\beta2$*breeding_status (1|individual)
5. Sex and breeding status interacted to influence distance travelled from the nest	Distance from nest $\sim\beta_0 + \beta_1$*sex + β_2*breeding_status + β_3*(sex:breeding_status) + (1|individual)

to high nest site fidelity (Berigan et al., 2012). We compared distance travelled from the nest between sexes and between breeding and non-breeding birds, using the same methods and hypotheses used for the homerange size analysis described above, except that distance traveled was the response variable and individual owl was included as a random effect (Table 1). Models were fit using distance from nest as the response variable and the Gaussian family with a log-link.

2.5. Foraging habitat selection

To evaluate foraging habitat selection, we tested whether owls used habitats disproportionately to the amount available (Johnson, 1980) by comparing intensity of habitat use to availability of habitat (Thomas and Taylor, 2006). We restricted our analysis to two measures of forest structure (canopy cover and dominant tree size) that are known to be highly important for California Spotted Owls (Call et al., 1992; Williams et al., 2011), however we acknowledge that habitat selection for this species comprises a much wider range of factors including other components of habitat structure (North et al., 2017), fire history (Bond et al., 2016, 2009), prey availability, habitat configuration (Eyes et al., 2017), and presence or water or riparian areas (Bond et al., 2016), as well as conspecific and interspecific interactions. We assessed habitat selection by foraging owls at four spatio-temporal scales: landscape (2nd order), home range (3rd order), foray, and nightly (Johnson, 1980). We analyzed all owl movements using the R packages *BBMM v3.0* (Nielson et al., 2015), *adehabitatLT v3.3.0* (Calenge, 2006) and *adehabitatHR v3.3.0* (Calenge, 2006).

2.5.1. Landscape scale

To evaluate foraging habitat selection at the landscape scale, we tested whether owls used habitats disproportionately to the amount available by comparing habitat use at the home range scale to availability of habitat within the eastern or western (Fig. 1c) study areas. We characterized habitat using vegetation mapping data (U.S.D.A. Forest Service, 2015) based on the CALVEG ("Classification and Assessment with Landsat of Visible Ecological Groupings") classification (Nelson et al., 2015). From these spatial data we selected two habitat variables that have been associated with California Spotted Owl habitat use, are widely quantified, and are often targeted for manipulation by forest managers: percent canopy cover and dominant tree size (Blakesley et al., 2005; North et al., 2017). Areas of non-forested land, roads, water, and cleared or naturally open areas were categorized as "open treeless areas".

We treated four categories of canopy cover, three categories of dominant tree size, and open treeless areas as eight separate datasets. Canopy cover categories included high ($>$ 70%), medium (50–70%), low (30–50%) and very low ($<$ 30%). Dominant tree size was based on the mean size of the dominant trees in the stand, measured as diameter at breast height (DBH), categorized as large ($>$ 50 cm), medium (25–50 cm), or small ($<$ 25 cm). We delineated the landscape available to owls as the MCP of every foraging location obtained for all the owls in our study, separated into eastern and western landscapes to account for a substantial gap in used habitat near the center of our study area (Fig. 1c).

To quantify habitat use, we calculated volume of the Brownian bridge utilization distribution (UD) for each owl*season (Horne et al., 2007; e.g. Cox and Kesler, 2012a). The Brownian bridge method extends traditional methods of quantifying animal space use (e.g. kernel density, MCPs) by accounting for temporal autocorrelation among locations to estimate the probability density function (PDF) and utilization distribution (Calenge, 2006). When calculating UDs, we excluded time lags longer than 62 min (our longest nightly sampling interval), reduced our data to one location per hour (higher resolution data addressed below) and used a spatial accuracy of 30 m (corresponding to accuracy of our GPS units) and a grid cell size of 50 m. Within each UD, we calculated the volume of use within eight habitat categories (Fig. 1c, d) for each owl*season, and within available landscape (i.e., east or west). We produced a landscape-scale dataset for each of the 8 habitat categories, each with 22 owl*seasons of proportional used habitat, and 22 measurements of proportional owl*season available area (representing either the east or west landscape). We developed seven generalized linear mixed effects models to test hypotheses on foraging habitat selection (Appendix S2, models 1–7) and used model selection to determine the most parsimonious model. Territory was included as a random effect in all models. We retained the model with the lowest AIC_c as the best approximating, or the best set of models, if top models were within 2 ΔAIC_c (Burnham and Anderson, 2003). We evaluated the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and assessed whether it significantly improved model fit (reduced $\text{AIC}_c > 2$). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Test statistics were t values for single models and z values for model-averaged sets. Models were fit using proportion as the response variable, with the Gaussian family and the log link.

2.5.2. Home range scale

We used methods similar to those described above to compare

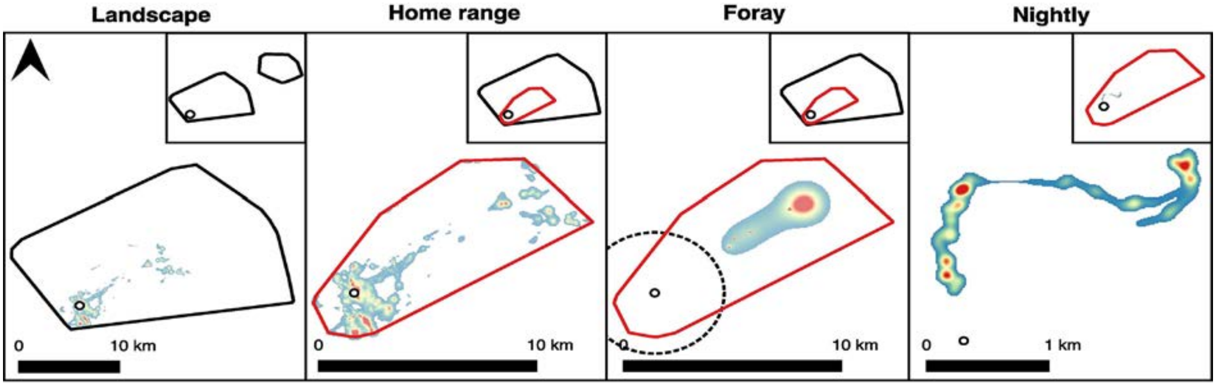

Fig. 2. Example of foraging habitat selection analysis at four spatio-temporal scales (landscape, home range, foray and nightly) for a nonbreeding female California Spotted Owl (1177–40374, Appendix S1) tracked during the 2016 breeding season (April 1–August 31) in the Sierra Nevada, California. At the landscape scale, the volume of use by owls in each habitat category, based on a utilization distribution (UD) for each owl*season (high use red to low use blue), was compared to the proportion of area for each habitat category (see text) within the western landscape of the study area (black polygon – see inset for both landscapes). Habitat use (volume of UD in each habitat category) was also compared to available habitat within the home range minimum convex polygon (MCP) for the owl*season; (red polygon). The foray scale compared volume of use by owls in each habitat category based on the UD of owls during forays to the proportion of habitat categories within the home range (red polygon). We defined forays as movements outside a 3.2-km buffer around the nest (dotted circle), the mean distance to nearest neighboring nest of study subjects. Foray and nightly scale insets show location of the home range within the western landscape. The nightly scale compared habitat use within the UD, for each night of high resolution data, to habitat availability within the home range (red polygon, see inset). Nest location is denoted by a black circle on all panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportional habitat use within the UD and available habitats within the MCP home range (Fig. 2). We produced a home range dataset for each of the eight habitat categories in the MCPs (available area) and 22 owl*seasons of proportional habitat use. We used the same habitat variables described above, and the same alternative models (Appendix S2, models 1–7) and model selection process. Mixed effect models were fit using proportion as the response variable, with the Gaussian family and the log link.

2.5.3. Foray scale

We examined habitat selection during forays, which occurred in six non-breeding females in our study. The mean distance to nearest neighboring nest of study subjects was 3.2 km, so we defined forays as movements farther than 3.2 km from the nest and temporally extending for ≥10 locations and 10 h. We estimated the proportional used area for each habitat with UDs for each foray*night (n = 18 in 6 owl*seasons), and compared those to the proportional area of each habitat within the MCP home range for the owl*season using a generalized linear mixed effects model that included individual as a random effect, using the Gaussian family and the log link. We used the same habitat categories described above with a similar model fitting and selection process, but examined only the effect of the habitat category (Appendix S2, models 1–2). Most birds were sampled hourly during forays, however we also included four foray nights with high resolution sampling (every 5 min). As a final step, we tested our models with and without the high resolution data and as we found no difference in the direction or significance of results, we retained the high resolution data.

2.5.4. Nightly scale

For 21 of the 22 owl*seasons, high resolution location data (locations recorded every 1–6 min) were available, enabling analysis of habitat use at the nightly scale. Nightly records ranged from 2.4 to 7.4 h periods over 103 nights (mean 6.4 h, 1.5 SD) and 88% of nights had > 6 h sampling. We obtained a mean of 87 (SD 12.6, range 72–126) locations within each sampling period. We derived a UD for each owl night and estimated the proportional used area by habitat. We used the same available area as for home range analysis, the MCP, and included individual owl as a random effect. We used the same habitat categories described above, the same model fitting and selection process, and similar alternative models (Appendix S2, all models).

2.6. Roost habitat selection

We evaluated owl selection of roost habitat by comparing used and available habitat with package *adehabitatHS v0.3.13* (Calenge, 2006). Roost locations were defined by the location temporally closest to 1200 h for each owl from the set of locations recorded between 2 h after sunrise and 2 h before sunset. We summed the number of roost locations within each habitat category for each owl*season to define use. Available roost habitats were defined as the proportion of each habitat category within the corresponding MCP home range. We then calculated Manly selectivity measures for each habitat category and tested overall habitat selection using a log-likelihood test statistic (Khi2L) (Manly et al., 2007). We treated canopy cover and dominant tree size as separate categorical variables, both of which included open treeless areas as a variable level. Manly selection ratios were interpreted as indicating selection for a habitat if the ratio and its confidence interval was > 1 and selection against a habitat if the ratio and its confidence interval were < 1. We used a type III test because the use and availability were measured for each owl*season (Thomas and Taylor, 1990).

2.7. Protected activity center analysis

We analyzed overlap between PACs and owl home ranges, and selection for or against PACs, using foraging space use (volume of use) and roost locations. PACs (designated to comprise the best available 121 ha of owl habitat surrounding known and suspected nest stands) were delineated in previous years by Forest Service biologists. For each owl*season we identified the “nest PAC” as the PAC that contained the nest, or the previous year’s nest for non-breeding birds, and “all PACs”, or sections of PACs, intersected by the MCP home range.

We compared PAC use (UD volume within PAC/s) with the percent area of PACs within each owl's MCP home range (available) for all owls, regardless of reproductive status (22 owl*seasons). We used a method similar to the foraging habitat selection analysis to test for selection for or against PACs. To assess the overlap of PACs with roost locations, we used a similar approach, but rather than intersecting PACs with volume of foraging space use, we intersected PACs with roost locations for 15 out of the 22 owl*seasons for which there were > 20 roost locations. We used Manly selectivity measures to compare proportional use of PAC and non-PAC areas, using number of roost sites within and outside PACs (used) and percent area of PACs within each owl's MCP home

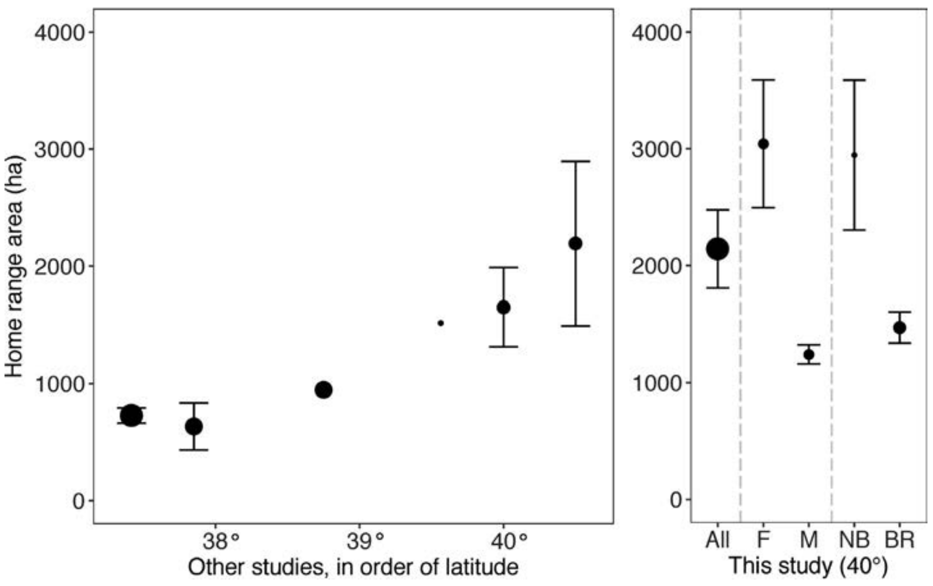

Fig. 3. California Spotted Owl breeding season (1 April–31 August) home range (MCP) estimates and SE (whiskers) reported elsewhere in the Sierra Nevada (left) (from Roberts, 2017, references listed below), and reported herein [this study] for the Plumas National Forest during 2015–2017 (right). Other studies, ordered by latitude, were conducted in Sierra National Forest (Zabel et al., 1992); Yosemite National Park (Eyes, 2014); Eldorado and Tahoe National Forests (Williams et al., 2011); Tahoe National Forest (Call et al., 1992); Plumas National Forest (Gallagher, 2010); and, Lassen National Forest (Zabel et al., 1992). Dot-size represents sample size, which ranged from n = 5 (Tahoe National Forest) to n = 22 (this study). We report estimated homerange sizes by sex and breeding status for birds evaluated herein as arithmetic means and SE of observed data for comparison to other studies, though this differs from least squared means reported in the text. Only studies using the 100% minimum convex polygon method to calculate home range were included to facilitate comparisons.

range (available), using the same test statistic as for roost selection analysis (Khi2L).

3. Results

3.1. Homerange size

Mean California Spotted Owl homerange size (2143 ha, 334 SE) was similar to estimates from previous studies within the Plumas National Forest (1653 ha, 336 SE) and the adjacent Lassen National Forest (2195, 701 SE; Fig. 3). Mean kernel density estimates of home range (2319 ha, 442 SE) were 8% higher than minimum convex polygon estimates. Homerange sizes differed significantly by sex (TS = 3.74, $p < 0.001$) and breeding status (TS = 1.97, p = 0.049) (Appendix S3). For the sex-only model, least squared mean home range of female owls (2611 ha, 95% CI 1961–3476) was more than double mean male home range (1216 ha, 95% CI 914–1619). Survey year did not influence home range size as the best models outranked the models including year.

3.2. Distance travelled

Breeding owl maximum nightly transit distances (sum of all nightly movements) ranged from 12.3 (7.0 ± 1.9) km for males to 17.9 (8.3 ± 3.0) km for females. Nightly maximum transit distances for non-breeding owls ranged from 7.9 km for males (6.2 ± 1.1) to 32.1 km for females (8.6 ± 4.8). All non-breeding females travelled outside the home range of their mate (Fig. 4) and visited (location points were recorded within) a mean of 4.5 (range 3–6) PACs (Appendix S1), while their home ranges overlapped with 4.7 (3-8) PACs. One non-breeding female (1177–40,374; Fig. 4b, green) left her territory and forayed to locations > 10 km from the previous year's nest on her home territory on four occasions between 17 May and 31 August for periods of 2, 8, 21 and 2 days. During the forays she visited six PACs in total and passed through the adjacent home ranges of another marked owl pair (Fig. 4b).

Distances travelled from the nest (straight-line distance, not transit distance) by non-breeding owls differed between sexes, with sex and breeding status interacting significantly (Appendix S3). Female owls travelled 1.3 times farther from the nest (TS = 4.70, $p < 0.001$) than male owls (respective mean distances of 2.3 km, 95% CI 1.84–2.91; and 1.76 km, CI 1.38–2.25). Breeding status alone was not a reliable predictor of maximum distance travelled from nest (TS = 1.25, p = 0.221); however, the interaction between sex and breeding status

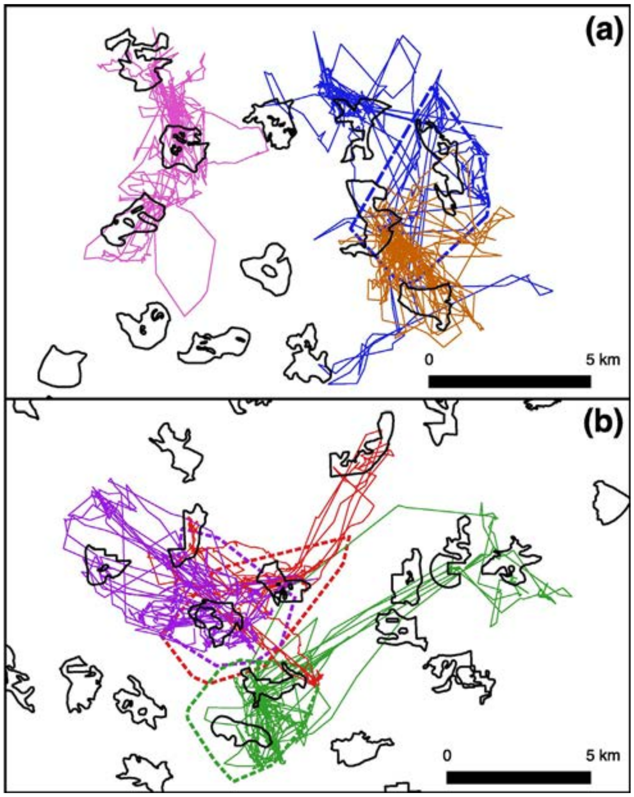

Fig. 4. Movement paths of six non-breeding female California Spotted Owls (traces), home ranges of mates in the same year (if tracked, dashed polygons) and Protected Activity Centers (black polygons). All owls presented in this figure were either non-breeding or had their nest fail in the season tracked and were tracked during breeding seasons (1 April–31 August) of 2016 and 2017. Panel (a) shows three non-breeding females in the eastern landscape (pink traces depict a female whose mate was not tracked, while blue and brown depict two females that paired with the same male, but in a different year). Panel (b) illustrates three non-breeding female*seasons from two territories in the western landscape (red and purple traces are from two separate female owls that paired with the same male in different years). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

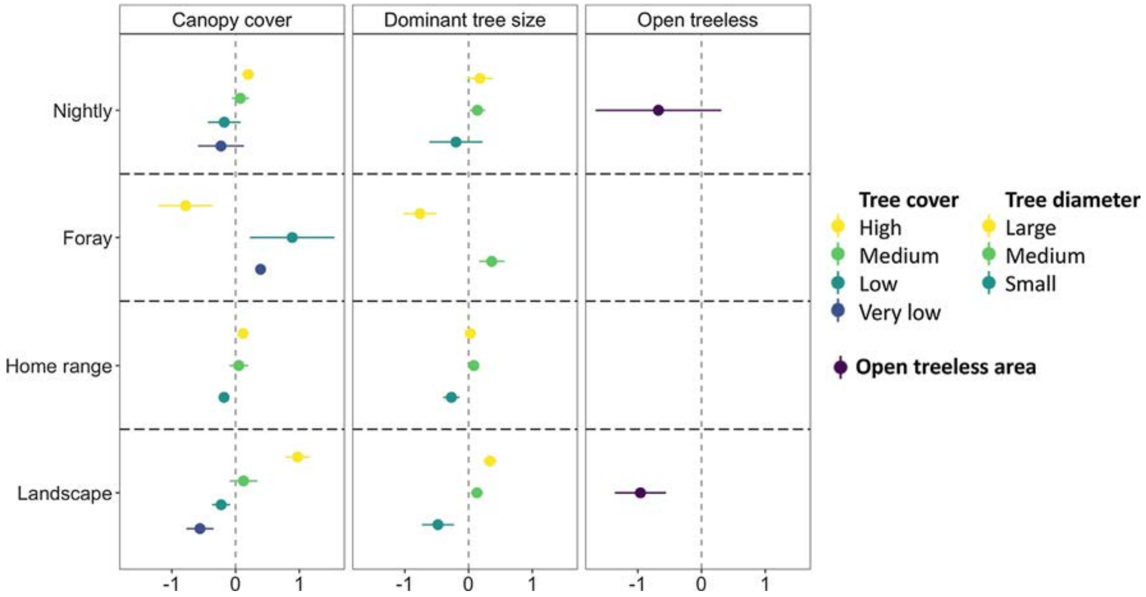

Fig. 5. Summary of best models describing habitat selection by California Spotted Owls during breeding seasons of 2015–2017 at four spatio-temporal scales, including landscape, home range, foray and nightly. Coefficients and 95% CI (whiskers) from top ranked models (or model-averaged model sets) that included the used/available categorical variable are shown. Positive coefficients indicate selection for a habitat category and negative coefficients indicate selection against. Three habitat categories are shown: canopy cover [high (> 70%), medium (50–70%), low (30–50%), very low (< 30%)], dominant tree size [large (> 50 cm), medium (25–50 cm), small (< 25 cm)] and open treeless areas (one category).

was significant (TS = −7.74, p < 0.001) due to greater distances travelled by female non-breeding owls (Appendix S4). Male owls travelled similar distances from the nest irrespective of breeding status (Appendix S4). Survey year did not influence distance travelled from the nest as the best model outranked the model including year.

3.3. Foraging habitat selection

After accounting for differences between sexes and breeding status, California Spotted Owls used habitats selectively at landscape, home range, foray and nightly scales. Survey year did not appear to influence foraging habitat selection, as only 3 models were improved by adding year (home range: open treeless area, nightly: very low cover, small dominant tree size), none of which demonstrated significant habitat selection (Fig. 5, Appendix S6). Landscape scale best approximating models indicated that owls selected for high canopy cover (TS = 10.1, p < 0.001), selected against low (TS = 3.1, p = 0.002) and very low canopy cover (TS = −5.1, p < 0.001) and used medium canopy cover in proportion to availability (Fig. 5, Appendices S5 and S6). Owls selected habitat at the landscape scale that was dominated by large (TS = 6.2, p < 0.001) and medium (TS = 2.7, p = 0.007) diameter trees, and selected against stands dominated by small trees (TS = −3.7, p < 0.001) or open treeless areas (TS = 4.7, p < 0.001). The best approximating landscape models for large trees included breeding status, however no landscape scale models included sex (Appendices S5 and S6). Models at the landscape scale had the greatest explanatory power among the three scales that included all owls (Landscape, home range, nightly; Appendix S5).

At the home range scale, after accounting for differences between sexes and breeding status, we found that owls selected for high canopy cover (TS = 3.7, p < 0.001), selected against low canopy cover (TS = 4.8, p < 0.001) and used medium and very low canopy cover in proportion to availability (Fig. 5, Appendix S6). Owls also selected habitat within the home range that was dominated by medium-sized trees (TS = 2.3, p = 0.022) and against stands dominated by small trees (TS = 4.1, p < 0.001), whereas stands dominated by large trees and open treeless areas were used in proportion to their availability (Appendices S5 and S6). The best fitting home range models for seven variables included breeding status and sex (Appendices S5 and S6).

In contrast to habitat selection at other spatio-temporal scales, six non-breeding females in our study selected against high canopy cover (TS = −3.6, p < 0.001) and large dominant tree size (TS = −5.7, p = 0.003) during forays, while selecting for areas with low (TS = 2.6, p = 0.009) and very low (TS = 12.3, p < 0.001) canopy cover dominated by medium sized trees (TS = 3.5, p < 0.001) (Appendices S5 and S6).

At the nightly scale, accounting for differences between sexes and breeding status, owls selected for high canopy cover (TS = 4.0, p < 0.001) and stands dominated by medium-sized (TS = 2.2, p = 0.025) but not large (TS = 1.7, p = 0.087) trees. All of the best approximating models or model sets for the nightly scale contained interaction terms with sex and/or breeding status, indicating differential selection between sexes and breeding/non-breeding owls (Appendices S5 and S6).

3.4. Roost habitat selection

Owls selected roost sites based on canopy cover (TS = 319, df = 28, p < 0.001) and dominant tree size (TS = 264, df = 23, p < 0.001). Owls selected for high canopy cover (Manly selection ratio = 1.61 [1.39–1.82]) and against areas with canopy cover < 50% (Fig. 6; Manly selection ratio for low = 0.10 [0.02–0.19], Manly selection ratio for very low = 0.06 [−0.02 to 0.13]). Owls also selected against stands dominated by small trees and open treeless areas for roosting (Fig. 6, Manly selection ratio for trees < 25 cm = 0.20 [0.12–0.28] and Manly selection ratio for open treeless areas = 0.09 [−0.08 to 0.27]). Habitat with medium canopy cover (50–70%) or dominated by either medium or large dominant tree sizes (> 25 cm), was used by roosting owls in proportion to availability in the home range (MCP), indicated by Manly selection ratios with intervals overlapping 1.0 (Fig. 6).

3.5. Protected activity center analysis

The PACs that contained the nest (or previous year's nest) encompassed a mean of 14.6% (range 3.7–31.6%, 1.5 SE) of owl*season UDs. When all PACs were considered, they accounted for a mean of

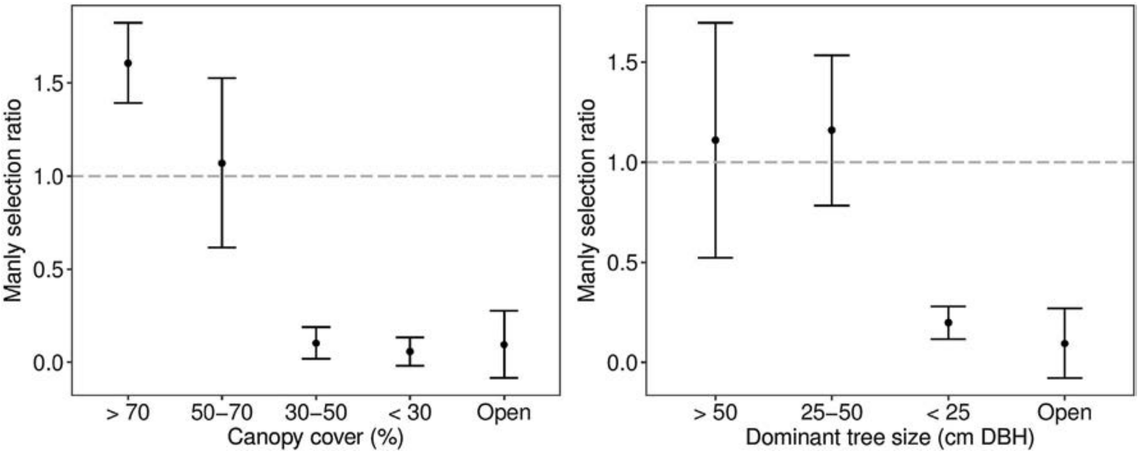

Fig. 6. Manly selection ratios showing positive (> 1) and negative (< 1) selection of canopy cover and tree size categories by roosting California Spotted Owls across 22 owl*seasons, during breeding seasons of 2015–2017.

22.1% (range 4.3–39.2, 1.6 SE) of owl*season UDs. Owls used multiple PACs throughout the breeding season with Owl*season UDs overlapping a mean of 2.7 PACs (range = 1–6), regardless of breeding status or sex [mean (range) number of PACs within owl UDs: breeding females = 2.2 (2–3), breeding males = 2.1 (2–3), non-breeding females = 4.5 (3–6), non-breeding males = 1.8 (1–2); Appendix S1]. The PACs containing nests (or containing nests during previous year) contained an average of 48% of roost sites used per owl (range 2.3–90.4, 8.0 SE), and the average proportion of roost sites contained within PACs did not increase significantly when all PACs were considered (mean of 49.8%, range 4.7–92.0, 8.0 SE). Owls selected for PACs while foraging, whether considering only the PACs containing their nest (*TS* = 3.8, p < 0.001) or all PACs (*TS* = 4.0, p < 0.001). Owls also selected for PACs while roosting, considering PACs containing their nest (TS = 638, df = 15, p < 0.001; Manly selection ratio = 6.35 [4.67–8.03]) or all PACs (TS = 372, df = 15, p < 0.001; Manly selection ratio = 3.13 [2.27–3.99]).

4. Discussion

High resolution GPS observations of the movements of California Spotted Owls confirmed the importance of late seral stage habitat (high canopy cover and large trees) for roosting and foraging at multiple scales and revealed previously undocumented foraying behaviors by non-breeding females during the breeding season. Our findings also highlight potential limitations of existing PACs in protecting owl habitat, as individual PACs overlapped with only 48% of roosts and 14.6% of foraging space use for owls that nested within them and individual owls visited up to 6 different PACs during one season.

The tendency of owls to select roost sites with greater canopy cover and larger diameter trees than foraging sites corroborates previous findings (Gutiérrez et al., 1992; Irwin et al., 2007; Kramer et al., 2016; North et al., 2017; Tempel et al., 2016). We found strongest evidence of foraging habitat selection at the landscape scale, where owls selected for substantial canopy cover (> 70%) and stands with medium to large trees (> 25 cm DBH), while selecting against low to very low canopy cover (< 50%), stands dominated by small (< 25 cm) trees, or open treeless areas (Fig. 5). Habitat selection at home range and nightly scales exhibited similar but weaker patterns, due to a stronger influence of sex and breeding status on habitat availability and selection, as well as variability among individual owls (Fig. 5, Appendices S5 and S6). Selection at finer scales (home range and nightly) may be limited by selection occurring at larger scales (Johnson, 1980), and others have reported strongest habitat selection at broader scales (Boyce et al., 2003; Stolen et al., 2007). We hypothesize that owls select high quality habitats at the landscape scale, potentially masking the importance of finer-scale habitat selection. However, weaker habitat selection relationships at finer scales also may be due to preferences for habitat features outside the focus of this study, such as forest edges (Eyes et al., 2017; Williams et al., 2011), burned areas (Bond et al., 2016, 2009), or riparian corridors (Bond et al., 2016; Irwin et al., 2007) or other factors including conspecific and interspecific interactions. In contrast to other spatio-temporal scales, our results indicated that California Spotted Owls selected for less dense vegetation (< 50% canopy cover) during forays. Foraying birds could have been attempting to minimize transit to known distant locations, or attempting to avoid encounters with other territorial birds during forays. Mobile species, such as Spotted Owls, rely on multiple patches of suitable habitat within their home range and often traverse environments that are unsuitable for some activities (Holloway and Miller, 2017). California Spotted Owl movement patterns indicated birds are likely able to acquire environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across the landscape, when the costs of gathering such information does not outweigh the benefits.

Our estimates of California Spotted Owl breeding homerange sizes were comparable with those observed for this subspecies in nearby Lassen National Forest (Zabel et al., 1992; Fig. 3). Our estimates were larger than breeding home range estimates of Mexican Spotted Owls (regional means of 228–562 ha; U.S. Fish and Wildlife Service, 2012) and of Northern Spotted Owls (regional means of 388–1150 ha; Carey et al., 1992; Forsman et al., 2015), with which they hybridize in the Northern part of their range (Miller et al., 2017). We found differences attributable to sex and breeding status (Fig. 3, Appendix S3), which have not previously been reported for California Spotted Owls (Roberts, 2017). Non-breeding females had the largest home ranges, the greatest of which was a 6496 ha breeding-season MCP, 5 times the mean reported in the literature (Roberts, 2017). Larger female home range is partially attributable to foraying behavior, wherein females left home territories and visited multiple (up to 6) surrounding PACs. One female transited > 30 km in a night, and undertook multiple forays of > 10 km while repeatedly visiting areas where she nested in previous years (Fig. 4b, green traces). Males may incur relatively greater costs (e.g. reduced territory defense) compared to females when using areas at great distances from the nest site, which could explain why we did not observe male forays. Foraging females are not likely seeking current year or future extra-pair copulations, as California Spotted Owls exhibit synchronous biennial cycles in reproductive output (Blakesley et al., 2010) and extra pair fertilizations are not commonly reported among owl species (Arsenault et al., 2002; Koopman et al., 2007; Lawless et al., 1997; Marks et al., 1999; Saladin et al., 2007). Rather, foraying may represent prospecting for future opportunites, an exploratory behavior pattern not previously documented in this species.

Prospecting, or gathering advanced information about potential breeding habitat within an area before settling there, has been described in > 100 bird species (Reed et al., 1999 and references therein). Accurate assessment of quantity, quality and configuration of available habitat is important to individual fitness, population dynamics and distribution (Howard, 1920; Lack, 1971; Reed et al., 1999; Wiens, 1976). Individuals must be able to acquire reliable environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across a landscape without costs of information gathering outweighing the benefits (Cox and Kesler, 2012b; Kesler et al., 2010; Johnson, 1989; Reed and Oring, 1992). Our documented foraying behavior may be a precursor to dispersal, given 7% of breeding California Spotted Owls in a nearby study dispersed into new territories between breeding seasons and 42% of breeding dispersals were into adjacent territories (Blakesley et al., 2006). A recent study noted observations of California Spotted Owls in multiple PACs during a breeding season, but did not examine the behavior in detail nor report sex or breeding status of birds (Berigan et al., in press). To our knowledge, foray behavior has not been recorded for the Mexican Spotted Owls and has been noted but not studied for the Northern Spotted Owl (Forsman et al., 2002). Investigations using VHF telemetry typically have not reported the frequency or duration of periods when birds went undetected, but inability to locate birds during VHF studies could indicate foraying behavior. Recent declines in Northern Spotted Owl natal dispersal distances of 1 km per year, alongside habitat fragmentation and increases in Barred Owl populations, indicate a more detailed understanding of multi-scale movements of all Spotted Owl subspecies afforded by GPS-tracking is likely an important component for their conservation (Hollenbeck et al., 2018).

Protection of owl core use areas (nesting and roosting sites) through exclusion of stand-altering activities within designated PACs is currently the management focus for California Spotted Owls. In addition to establishing PACs, the U.S.D.A. Forest Service designates up to 971 ha of the best available California Spotted Owl habitat in the closest proximity to a PAC as a “Home Range Core Area” (HRCA) (U.S.D.A. Forest Service, 2004), where owl habitat needs are to be considered in management decisions, but stand-altering vegetation management practices are allowable and routinely undertaken. Berigan et al. (2012) reported high overlap between PACs and core use areas based on long-term roosting and nesting data. Although our results indicated positive selection for PACs by foraging and roosting California Spotted Owls on the Plumas National Forest, we found relatively low overlap between PACs and both roost locations (< 50%) and foraging space use (< 25%). Indeed, for some owls < 5% of their foraging or roost locations were contained within the PAC in which they nested (or nested in the previous year). Furthermore, our estimates of owl home range size and distance travelled were restricted to the breeding season. Owls are likely to range over much wider distances annually, with PACs and even HRCAs consequently protecting only a small fraction of habitat used for complete annual life-history needs.

PACs were developed specifically to protect nesting and roosting sites, rather than the much broader foraging areas used by Spotted Owls. Nevertheless, California Spotted Owl populations continue to decline, particularly within study areas on National Forest lands (Blakesley et al., 2010; Conner et al., 2016; Tempel et al., 2016) for reasons that are not well understood but may include past and ongoing forest management activities (Jones et al., 2018; Tempel et al., 2017). Based on the relatively low overlap between PAC areas and roosting and foraging habitat use by the owls we studied, we hypothesize that insufficient habitat protection from stand-altering activities outside PAC areas could partially explain ongoing population declines. Most of the habitat used by owls for roosting and foraging in our study was outside of PACs and therefore available for stand-altering forestry activities. Even where PACs protect nesting stand conditions conducive to successful reproduction, stand-altering activities elsewhere in owl home ranges may reduce occupancy or reproductive success. For example, a simulation study by Tempel et al. (2015) found that stand-wide fuel-reduction treatments that reduced canopy cover had a negative effect on owl nesting habitat and demographic rates 30 years into the future in the absence of fire. The same study predicted positive effects of fuel reduction treatments on owl nesting habitat and demographic rates if fire occurred in the study area (Tempel et al., 2015). While limited research to date has not indicated negative effects of timber harvest on California Spotted Owl foraging (Irwin et al., 2015), harvesting can reduce populations of key California Spotted Owl prey (Lehmkuhl et al., 2006; Williams et al., 1992). Relationships between prey dynamics and owl fitness are still poorly understood (Roberts, 2017).

Cumulatively, past results combined with our findings suggest that habitat conditions throughout individual California Spotted Owl home ranges – but beyond the boundaries of PACs – may be critical for fulfilling life history needs, and if inadequate, could be contributing to ongoing declines. Additionally, even habitat outside usual home ranges may be more important than has been previously considered. Non-breeding female owls traveled great distances (forays), sometimes roosting and spending over a week > 10 km from their territory centers before returning. Although it would seem obvious that connectivity of later seral forest across the landscape is important for this species, our finding that foraying owls selected habitat attributes (< 50% cover) in contrast to those selected during non-foray movements requires further study. Understanding the role of long distance foray movements in facilitating breeding dispersal, as well as genetic and demographic connectivity, and more generally, the importance of habitat well outside what has historically been considered the activity center of California Spotted Owls, is likely important for addressing ongoing population declines.

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Data accessibility

Data will be available by request from Plumas National Forest at the conclusion of this ongoing study.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.017.

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Simulating Fire and Forest Dynamics for a Landscape Fuel Treatment Project in the Sierra Nevada

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Abstract: We evaluated an actual landscape fuel treatment project that was designed by local US Forest Service managers in the northern Sierra Nevada. We modeled the effects of this project on reducing landscape-level fire behavior at multiple time steps, up to nearly 30 years beyond treatment implementation. In addition, we modeled planned treatments under multiple diameter-limited thinning scenarios to assess potential impacts on fuel treatment effectiveness. The planned fuel treatments reduced modeled conditional burn probabilities substantially across the landscape relative to those for a scenario with no simulated treatments. This reduction relative to that for the no treatment landscape was evident approximately 20 years after simulated treatment implementation. Although diameter-limited thinning scenarios resulted in different residual forest stand structures, we detected no real differences in modeled landscape-level burn probabilities. The modeling adaptations we made with respect to fuel model selection and simulated ingrowth/regeneration over simulated time, as well as incorporation of variable winds in fire simulations, collectively contribute to a robust analysis of the study area. FOR. SCI. 57(2):77–88.

Keywords: wildfire modeling, fuels reduction, minimum travel time, fire exclusion

THE COMBINATION OF INCREASED susceptibility of forests to damaging wildland fire (Cooper 1960) and the homogenization of many forested landscapes across the western United States, resulting from fire exclusion policies (Hessburg et al. 2005), necessitate large-scale mitigation efforts. Land management obligations, along with numerous financial, administrative, and operational constraints, inhibit simply implementing such mitigation efforts, or fuel treatments, across entire landscapes (Weatherspoon and Skinner 1996, Stephens and Ruth 2005, Collins et al. 2010). Thus, there is a need to design an arrangement of discrete fuel treatments that collectively contribute to slow fire spread and reduce negative wildland fire effects across the intended landscape (Finney 2001, Ager et al. 2010). Several studies have explored various fuel treatment designs across landscapes, ranging from relatively continuous linear features (Weatherspoon and Skinner 1996, Agee et al. 2000) to regular, dispersed features (Finney 2001) to more complex, optimization algorithm-based treatment deployment (Finney 2007, Finney et al. 2007). Although these and other studies (Ager et al. 2007a, 2007b, Schmidt et al. 2008) compare fuel treatment arrangements and offer suggestions for managers implementing treatments across landscapes, there remains a disconnect between these well-supported theories and actual implementation. This disconnect is a result of area restrictions/constraints on management activities, project appeals, and lack of expertise to assemble necessary data and run models (Collins et al. 2010, Moghaddas et al. 2010).

In this study we evaluated an actual landscape fuel treatment project (called the Last Chance project) that was designed by local US Forest Service managers on the Tahoe National Forest, California, USA. This project presented an opportunity to analyze potential landscape-scale effects of a typical fuels treatment project in the region. The objectives of the project were to reduce the potential for large and destructive wildfires, and improve forest resilience to other disturbance agents and stressors. We evaluated the effectiveness of this fuel treatment project at reducing landscape-level fire behavior, specifically conditional burn probabilities. To gain insight into the duration of fuel treatment effectiveness, we evaluated burn probabilities for 30 years into the future. We intend this portion of our analysis to provide managers with estimates of landscape-scale fuel treatment longevity, i.e., how often they can expect to either maintain treated areas or establish new fuel treatments. Finney et al. (2007) demonstrated a treatment rate of 2% per year (treating 20% of the landscape every 10 years) results in consistent reductions in fire growth. We intend to compare these findings with those from our own analysis based on a one-time treatment that is simulated into the future.

In response to ongoing debates regarding retention of

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large trees such that forest structure resembles more old forest characteristics, we additionally simulate the Last Chance project treatments by varying the upper tree diameter limit for cutting within the proposed thinning treatments. Stephens and Moghaddas (2005) and North et al. (2009) concluded that removing trees above the range of 25.4 to 40.6 cm (or 10 to 16 in.) dbh is not necessary for attaining fuel management objectives. We investigated three different diameter-limited thinning scenarios, 30.5 cm (12 in.), 50.8 cm (20 in.), and 76.2 cm (30 in.), for potential differences in residual forest stand structure and modeled landscape-scale burn probabilities. These three scenarios reflect the diameter limits imposed in the different Sierra Nevada-wide Forest Service planning documents (US Department of Agriculture 2001, 2004). We hypothesized that thinning only those trees 12 in. and less may not reduce stand susceptibility to fire, particularly at higher flame lengths, relative to 20- and 30-in. diameter limits on thinning.

Methods

Study Area

The Last Chance study area is located within the Tahoe National Forest and is situated in the northern Sierra Nevada (Figure 1). The climate is Mediterranean with a predominance of winter precipitation, a majority of which is snow, averaging 1,182 mm/year over the period of record 1990–2008 (Hell Hole Remote Automated Weather Station). Our core study area is defined by the boundaries of two adjacent watersheds in which landscape fuel treatments are scheduled for implementation between 2009 and 2011. This core area is approximately 4,300 ha, with elevation ranging from 800 m in the southwest to almost 2,200 m in the northeast portion of the study area. For fire modeling purposes (explained in the Fire Modeling section), we augmented the core study area with a square buffer that was a minimum of 1 km from the core area edge (Figure 1). The total buffered study area was 15,500 ha. Vegetation on this landscape is typical of west-slope Sierra Nevada: a mixed-conifer forest dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*) with sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*) appearing as a codominant at variable densities throughout. Stands of montane chaparral are interspersed throughout the area. Seven percent of the study area (approximately 300 ha) is classified as nonconifer forests, based on the Tahoe National Forest criteria (conifer trees constitute <10% of the tree crown area). Tree density varies by fire and timber management history, elevation, slope, aspect, and edaphic conditions. Fire history, inferred from fire scars recorded in tree rings, suggests a fire regime with predominantly frequent, low-severity fires occurring at intervals ranging from 5 to 15 years (Stephens and Collins 2004).

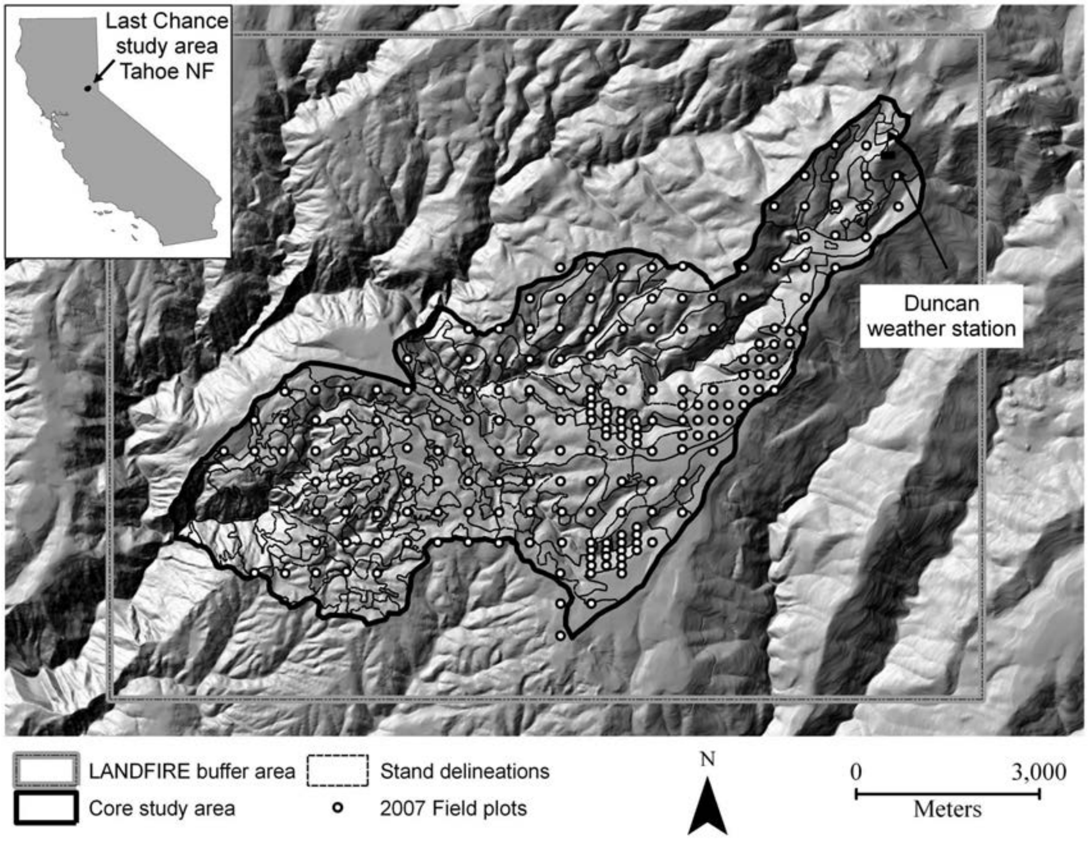

Figure 1. Field plot locations and stand delineations within the Last Chance study area, Tahoe National Forest, California. We used data from LANDFIRE (2010) to buffer the Last Chance study area for fire modeling. We obtained weather data for fire modeling from the Duncan Remote Automated Weather Station, which is also identified.

Field Sampling

We systematically established field plots at 500-m spacing across the Last Chance core study area, except the southwest corner of the core area due to extreme topography (Figure 1). We augmented sampling to 250- and 125-m spacing in areas more intensively studied as part the larger Sierra Nevada Adaptive Management Project (University of California Science Team 2009), resulting in a total of 199 sampled field plots. Plots were circular with an area of 0.05 ha and were navigated to using handheld global positioning systems (GPS). At each plot we recorded the slope, aspect, and GPS-derived elevation. We used three different sampling intensities based on tree size: $\geq$19.5 cm (throughout plot, 500 m^2), 5.0–19.4 cm (random one-third of plot, 167 m^2), and $<$5.0 cm (random belt transect, 76 m^2). We recorded tree species, vigor, crown position, dbh (1.37 m), total height, and height to live crown base (live trees only) for all trees in the upper two size classes. In the smallest tree size class, we recorded species and dbh. In addition, at each plot we cored, aged, and measured the height of a representative site tree to characterize differences in productivity across the study area.

We sampled downed woody, litter, and duff fuels on three randomly chosen transects within each plot. We used the line-intercept method to sample downed woody fuels (van Wagner 1968, Brown 1974). We measured duff, litter, and overall surface fuel depths at two points along each transect. We calculated fuel loads using the species-specific coefficients reported in van Wagtendonk et al. (1996, 1998), weighted by the proportion of total basal area of each species (Stephens 2001). On the same three transects we measured woody shrubs for cover (using transect intersections) and average height. We also made ocular estimates of total percent ground surface covered by herbaceous plants at each plot.

Modeling Forest Dynamics and Fuels Treatments

We used the Forest Vegetation Simulator (FVS) (Wycoff et al. 1982) with the Fire and Fuels Extension (FFE) (Reinhardt and Crookston 2003) to model fuel treatments under multiple diameter-limited thinning scenarios and to grow both treated and untreated forest stands into the future. We used the Timber Strata layer provided by the Tahoe National Forest to delineate individual stands (J. Babin, Tahoe National Forest, pers. comm., May 10, 2008). This geographic information system layer consisted of polygons, or stands, containing relatively similar forest composition and structure (n = 187). The stand delineations were based on aerial photo-interpreted classes of species, dominant tree size class, and tree density. Forest Service stands were used as the analysis unit rather than raster or grid cells to approximate the modeling used by Forest Service managers planning fuel treatment projects. Thus, the approaches we present may be more readily incorporated in actual land management planning. We "populated" each stand with trees sampled in the nearest field plot(s), either within or adjacent to each stand. We did not use a statistical imputation technique; plots were manually assigned for all 187 stands. For stands classified as plantations (n = 55), we used the nearest plot that fell wholly within a plantation (n = 20). As a result, some plots were used to populate multiple stands. In total, 199 plots were used to generate tree lists for 187 stands.

We simulated fuel treatments as prescribed in the Silviculturist Report prepared by the American River Ranger District, Tahoe National Forest (K. Jones, Tahoe National Forest, pers. comm., Jul. 29, 2008). This report identifies the individual stands to be treated and contains prescriptions for thinning and subsequent treatment of surface fuels, mastication, and underburning. Using multiple series of FVS and FFE keywords, we were able to match these prescriptions for our simulations. In general, the prescriptions call for treating 25% of the landscape (1,069 ha) by thinning from below, followed by mechanical/hand piling and burning (731 ha [17% of total]), mastication of shrubs and small trees (primarily within 20- to 30-year-old plantations: 105 ha [2.5%]), and underburning (233 ha [5.5%]). To investigate a potential effect of varying thinning diameter limits on overall landscape fuel treatment effectiveness, we used three different upper tree diameter limits, which were also associated with three different residual canopy cover targets. These targets also came from Forest Service planning documents (US Department of Agriculture 2001, 2004): 30.5 cm dbh (12 in.) and 60% canopy cover, 50.8 cm dbh (20 in.) and 50% canopy cover, and 76.2 cm (30 in.) and 40% canopy cover. Simulated thinning treatments involved thinning from below to a desired canopy cover target, such that no trees above the imposed diameter limit are cut. In other words, smaller trees are cut first and then progressively larger trees, but below the imposed diameter limit, until the overall canopy cover target is met. In a few cases the imposed diameter limit prevented achieving the stated canopy cover target; however, this was rare. The mastication and underburning treatments were unchanged for the three diameter limit/residual canopy cover scenarios.

We simulated the three diameter limit/residual canopy cover scenarios, along with a no treatment scenario, for four 10-year cycles. We modeled treatments according to the schedule projected by the Tahoe National Forest: thinning and mastication in 2009 and prescribed burning in 2010. FFE generates estimates of forest stand structural characteristics and surface (litter and downed woody) fuel loads, which we used as inputs for fire behavior modeling for four time steps using the ArcFuels interface: (1) 2007, pretreatment baseline; (2) 2017, first cycle after treatments; (3) 2027, second cycle after treatment, and (4) 2037, third cycle after treatment. Although thinning and mastication treatments were scheduled in 2009, FVS actually "implements" the treatments at the beginning of the cycle in which they occur. This means that in our simulations thinning and mastication actually occurred in 2007, whereas the prescribed burns were simulated as scheduled (i.e., 2010). As a result, our first posttreatment output (2017) does not represent immediate posttreatment; it represents 10 years postthinning and 7 years postburning. We could have simulated two shorter FVS cycles (3 and 7 years) to obtain more immediate posttreatment results; however, to keep growth cycles consistent throughout the simulation period and maintain consistency with underlying FVS growth models (Dixon 2002), we only used 10-year cycles. The forest and fuel parameter estimates output from FVS were then used to create the necessary stand structure/fuel input layers required by the fire behavior and spread model FlamMap (Finney 2006).

In the western Sierra variant of FVS, establishment of new trees in the absence of disturbance or ingrowth is not explicitly modeled. To simulate ingrowth, users must input the number, species, and frequency of establishment events. We modeled ingrowth for untreated stands in each cycle that favored shade-tolerant species, based on recommendations from Forest Service silviculture personnel within the region (R. Tompkins, Plumas National Forest, pers. comm., Jan. 5, 2009). We used a random number generator to choose the actual number of seedlings, within species-specific bounds, that established for a given stand, in a given FVS cycle. In addition, we regulated seedling height growth to simulate more realistic conditions under an intact canopy. We evaluated tree densities and stand canopy base height estimates to ensure that our ingrowth/regeneration assumptions were consistent with our own observations in the field and with local managers' knowledge of the study area. In the absence of any ingrowth/regeneration, stand canopy base heights increased considerably over time in untreated stands, which occurred at a rate that is difficult to justify ecologically, especially given the large proportion of shade-tolerant species present in many stands.

Fuel Model Selection

FFE explicitly models surface fuels at each time step, taking treatment effects on the various fuel loads into account. On the basis of the loads and distributions among fuel particle size classes and on other stand characteristics, FFE assigns fuel models to stands (Reinhardt and Crookston 2003). Our initial fire modeling runs and our familiarity with the Last Chance study area led us to conclude that the FFE fuel model assignments were not valid. Among other issues, crown fire activity and conditional burn probability under the no treatment alternative declined substantially over time. Seli et al. (2008) similarly expressed concern with FFE fuel model selection, and thus they created their own selection logic. We used some of the same criteria to develop our own fuel model selection logic. However, our approach involved using field plot-derived forest stand structure characteristics and site productivity to approximate stand fuel conditions. We used the statistical software package R to construct individual regression trees (De'ath and Fabricius 2000) predicting three plot-derived fuel variables: surface fuel load (includes litter and 1-, 10-, and 100-hour fuels), shrub cover, and coarse fuel load (1,000-hour fuels). We used basal area, tree density, canopy cover, dominant tree height, and site index summarized for each plot as predictor variables. Regression trees are ideal for such an analysis because they identify break values for predictor variables that can be used to repeatedly assign fuel models to stands. Statistical fits were moderate (R^2 = 0.21–0.27) but were deemed appropriate for "binning" stands into discrete Scott and Burgan (2005) fuel models. Figure 2 displays our final fuel model selection logic based on results from the individual regression trees. The chosen fuel models for each terminal point in the selection logic were based on input from local fire managers and on our familiarity with the study area after two extensive field seasons. See Table 1 for descriptions of fuel models used and their proportions throughout the study area over the duration of simulations.

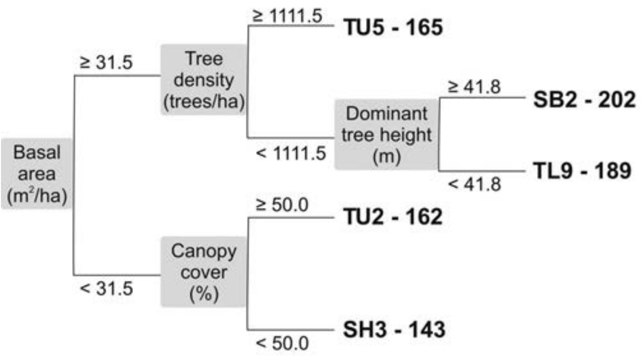

Figure 2. Surface fuel model selection logic for Last Chance stands. This logic did not apply to all treated stands in 2017 or to thinned/prescription-burned stands in 2027. The break values for the logic were determined from three separate regression tree analyses (see Methods for explanation). Surface fuel models were selected from Scott and Burgan (2005) and are identified in bold by code and number.

Posttreatment fuel models for treated stands were based on separate logic involving treatment type and time since treatment. In the first and second cycles after treatment, thinned stands were assigned timber-litter fuel models with progressively higher fuel loads (Table 1). Slash models were not assigned to thinned stands because of the prescribed and simulated modification of surface fuels after thinning. Stands that were underburned followed a similar progression of timber-litter fuel models but with slightly lower fuel loads (Table 1). By the third cycle, both thinned and underburned stands entered into the general logic used for untreated stands (Figure 2). Masticated stands were assigned a timber-litter fuel model with moderate litter and downed woody fuel loads in the first cycle after treatment (Table 1). For subsequent cycles, masticated stands were entered into the general fuel model selection logic described in Figure 2.

Fire Modeling

We used a command-line version of FlamMap (Finney 2006) called RANDIG to model fires across the Last Chance landscape. RANDIG uses the minimum travel time method (Finney 2002) to simulate fire spread based on user inputs for number/pattern of ignitions, fire duration, wind speed and direction, fuel moistures, topography, stand structure, and fuels. For each scenario and time step, we simulated 5,000 randomly placed ignitions, burning for 240 minutes (one 4-hour burn period). This burn period duration was selected such that simulated fire sizes (for one burn period) approximated large spread events (daily) observed in actual fires that occurred near the study area (Ager et al.

Table 1. Fuel model assignments for stands within the Last Chance study area and their proportion throughout the study area over the simulation duration

Scott and Burgan (2005) fuel model	Description of stands with fuel model assigned	Pretreatment (2007)	2017		2027		2037	
			NoTrt	Trt	NoTrt	Trt	NoTrt	Trt
143	Low basal area, low canopy cover	0.09	0.29	0.26	0.12	0.13	0.08	0.12
162	Low basal area, high canopy cover	0.41	0.09	0.09	0.04	0.03	0.01	0.02
165	Moderate to high basal area, high tree density	0.24	0.31	0.22	0.40	0.30	0.48	0.39
181	Post-prescribed fire (first cycle)	—	—	0.05	—	—	—	—
183	Post-prescribed fire (second cycle) Post-thin/pile burn (first cycle)	—	—	0.17	—	0.05	—	—
184	Postmastication (first cycle)	—	—	0.02	—	—	—	—
185	Post-thin/pile burn (second cycle)	—	—	—	—	0.17	—	—
189	Moderate to high basal area, moderate to low tree density, moderate to low site productivity	0.25	0.30	0.18	0.43	0.31	0.41	0.45
202	Moderate to high basal area, moderate to low tree density, high site productivity	0.01	0.01	0.01	0.01	0.01	0.02	0.02

Fuel model selection logic was based on multiple regression tree analyses using plot-level data for both dependent variables (fuel loads by category) and independent variables (forest structure attributes).

Trt, with simulated treatments; NoTrt, without simulated treatments.

2010). There were two fairly recent fires that burned near the Last Chance study area for which daily spread information existed: the 2001 Star fire and the 2008 American River complex. The largest daily spread event for each of these fires was approximately 1,300 ha, which was under the range of average simulated fire sizes for our no treatment scenarios: approximately 1,500–2,100 ha. Given that we only have two fires from which to compare large spread events and that in other areas of the Sierra Nevada daily fire growth in excess of 2,000 ha has been observed in recent fires (Fites et al. 2007, Dailey et al. 2008), we believe our burn period calibration represents a reasonable "middle ground" for large spread events in Sierra Nevada mixed-conifer forests.

We obtained weather information from the Duncan Peak Remote Automated Weather Stations, restricting the analysis period to the dominant fire season for the area (June 1–September 30). Observations were available from 2002 to 2009. We used 90th percentile and above wind speeds, based on hourly observations, to generate multiple wind scenarios under which fires were simulated. We identified the dominant direction and average speed of all observations at or above the 90th percentile value, 24 km hour^{-1}. This resulted in four different dominant wind directions, each with its own wind speed and relative frequency (based on the proportion of observations recorded at or above the 90th percentile value for each dominant direction) (Table 2). The modeled wind speeds were similar to those recorded during large spread events in two relatively recent and nearby fires: 2001 Star fire and 2008 American River complex. We used 95th percentile fuel moistures, as these are the conditions associated with large fire growth and difficulty in control.

We derived the necessary topographic inputs, slope, aspect, and elevation, using a 30-m digital elevation model obtained from the National Elevation Dataset (US Geological Survey 2006). Stand structure and fuels layers were derived from FVS outputs. For each stand, at each time step, FVS outputs for canopy cover, canopy bulk density, canopy base height, and dominant tree height, along with a fuel model assignment (computed outside of FVS), were compiled to develop continuous layers for each of these five variables across the core Last Chance study area. This resulted in 12 different simulated landscapes: no treatment (NoTrt), 30.5 cm (12 in) dbh thinning limit (Trt12), 50.8 cm (20 in) dbh thinning limit (Trt20), and 76.2 cm (30 in) dbh thinning limit (Trt30), all at three time steps (2017, 2027, and 2037). In addition, we ran a pretreatment baseline landscape for 2007, totaling 13 different simulated landscapes.

Table 2. Weather parameters for fire simulations using RANDIG

Weather parameter	Speed (km h^{-1})	Direction (° azimuth)	Relative frequency	Percent
Winds	29	180	0.31	
	31	90	0.31	
	27	135	0.31	
	27	315	0.07	
Fuel moisture				
1 h				2
10 h				3
100 h				5
Live herbaceous				30
Live woody				60

Parameters were drawn from the Duncan Peak Remote Automated Weather Stations and represent the 90th percentile and above winds and the 95th percentile fuel moistures for the predominant fire season in the area (June 1–September 30).

To allow for ingress and egress of simulated fires we buffered the irregularly shaped core study area using a rectangle that was a minimum of 1 km for the core area edge (Figure 1). Doing so ensured that certain areas were not "sheltered" from simulated fire spread. Because our field plots were confined to just the core study area, we were unable to use the same approach toward modeling forest dynamics over time for the buffer area. We opted to use

LANDFIRE (2010) vegetation and fuels layers for the area outside the core study area. The drawback of this approach is that LANDFIRE layers remain static throughout the simulation duration. Given that for our analyses we extract the RANDIG output from only the core area, we believe the impact of the buffered area layers being both from a different source and static is likely to be small.

For each simulated landscape, RANDIG outputs conditional burn probabilities, both overall and proportional for 20 flame length classes (0–10 m in 0.5-m increments) for individual 60-m pixels, spanning the entire buffered study area. Conditional burn probabilities are computed by dividing the total number of times a pixel burned by the total number of simulated fires ($n = 5{,}000$). To separate out more problematic simulated fire occurrence, both from a fire effects and a fire suppression standpoint, we only performed analysis on the burn probabilities for which modeled flame lengths were >2 m. Flame lengths >2 m typically correspond with crown fire initiation and present substantial challenges for suppression efforts (National Wildfire Coordinating Group 2004). We imported conditional burn probability surfaces, for modeled flame lengths >2 m, into ArcGIS software for further data analysis. For each of the 13 simulated landscapes we computed overall mean conditional burn probability, only using those pixels within the Last Chance core study area. To estimate potential offsite effects from treatments we extracted conditional burn probability pixel values within three distance ranges outside treatment boundaries. We used the Multiple Ring Buffer tool in ArcToolbox to construct concentric, nonoverlapping buffers extending 0–299, 300–599, and 600–900 m from treatment boundaries. Within each ring buffer we calculated mean conditional burn probabilities, again using only those probabilities associated with flame lengths >2 m.

Results

Simulated Stand-Level Treatments

Under each of the three diameter-limited thinning scenarios, stand averages for tree density, basal area, canopy cover, and canopy bulk density decreased, whereas canopy base height increased, relative to the NoTrt scenario (Figure 3). It is important to note that initial (pretreatment) canopy cover estimates (2007) for the thinned stands averaged near 50%, and as a result the canopy cover targets in the less intensive thinning scenarios (60% for the 30.5-cm dbh limit and 50% for 50.8-cm dbh limit) were already met for several stands (Figure 3). In such stands, simulated thinning primarily involved removing understory trees. This removal of trees is evident in the density changes for all three thinning scenarios after treatment (Figure 3). The stand structural changes in each of the thinning scenarios relative to the NoTrt scenario persisted throughout the simulation duration, with canopy base height being the only exception. In 2037 average canopy base height for all three thinning scenarios was nearly indistinguishable from that for the NoTrt scenario. Tree density, basal area, canopy cover, and canopy bulk density among the three diameter-limited thinning scenarios followed a nearly linear decreasing trend as the thinning diameter limit increased for all three modeled time periods (Figure 3).

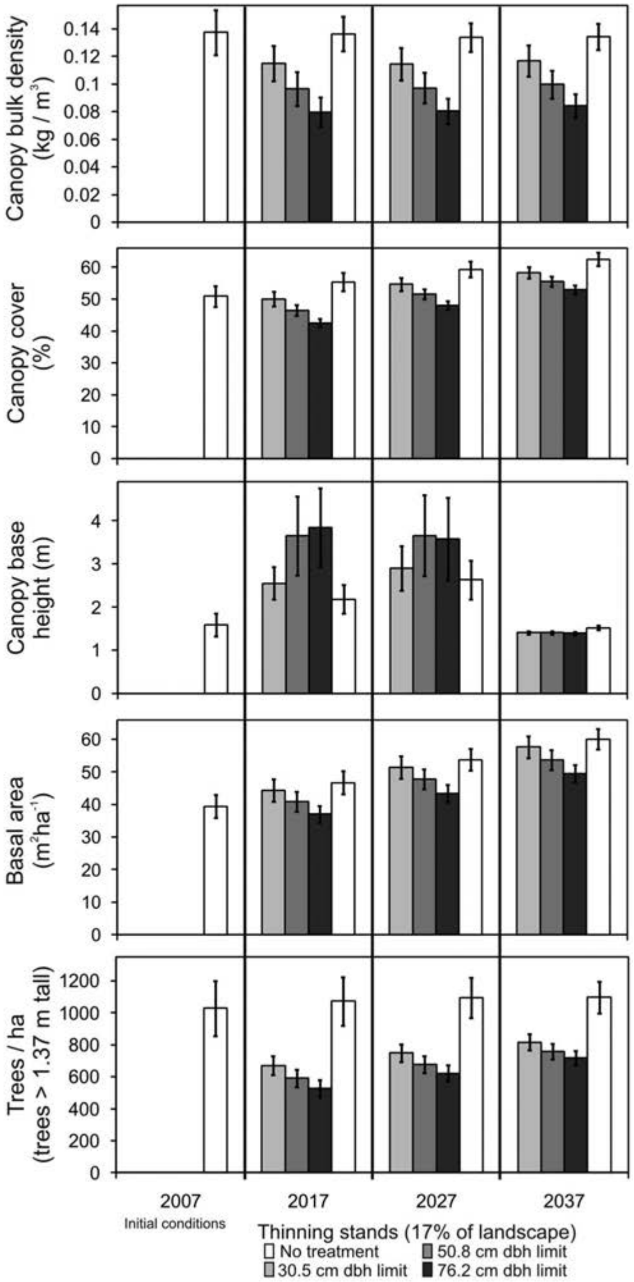

Figure 3. Average forest stand structural attributes for stands planned to undergo thinning. Thinned stands are simulated under three diameter-limited scenarios as well as a no treatment scenario for the same stands. Error bars represent 1 SEM. Attributes were derived from the Forest Vegetation Simulator, using tree lists for each stand based on our field inventory plots. The thinned stands represent 17% of the Last Chance landscape.

Tree density, basal area, canopy cover, and canopy bulk density decreased substantially for mastication and prescribed fire stands as well (Figure 4). The persistence of these effects, relative to the same stands modeled with no treatment, was evident for all three time periods and appeared generally stronger than that for the thinned stands. Initial canopy cover and canopy base height estimates in mastication stands were lower than those for all other

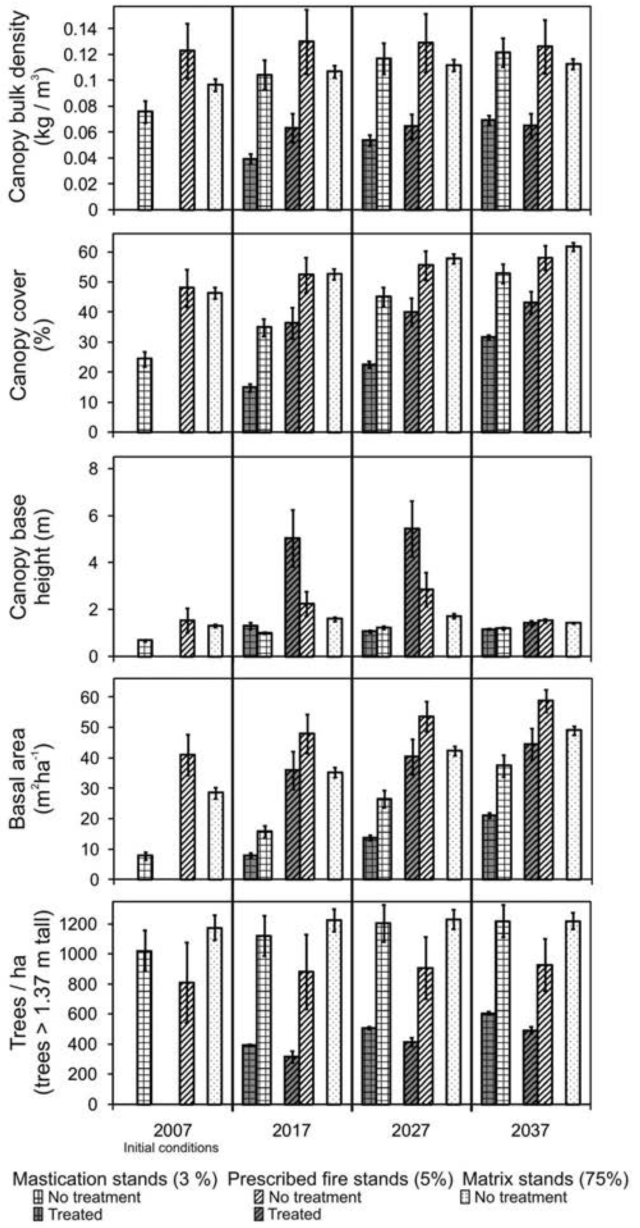

Figure 4. Average forest stand structural attributes for stands planned to undergo mastication treatment and prescribed fire treatment, as well as a no treatment scenario for the same stands. The stands planned for mastication and prescribed fire represent 3 and 5% of the Last Chance landscape, respectively. Structural attributes for stands within the study area that are not to be treated, referred to as matrix, are reported as well, representing 75% of the landscape. Error bars represent 1 SEM. Attributes were derived from the Forest Vegetation Simulator, using tree lists for each stand based on our field inventory plots.

stands, demonstrating differences in stand structure for the approximately 20- to 30-year-old plantations (2007 in Figures 3 and 4). In the first and second cycles after treatment implementation (2017 and 2027) canopy base height in prescribed fire stands increased dramatically (Figure 4). By the final time period, canopy base height in mastication and prescribed fire stands was similar to that in NoTrt and matrix stands (Figure 4).

Simulated Landscape-Level Fire Spread

The simulated treatments reduced conditional burn probabilities (flame lengths >2 m) not only within treatment areas, but also throughout the Last Chance study area (Figure 5). This reduction relative to the pretreatment scenario (2007) was evident across the Last Chance study area in both 2017 and 2027 (Figure 5). Analysis of burn probabilities in the three distance ranges outside the treated areas confirmed this reduction relative to the pretreatment condition and demonstrated only moderate increases in average conditional burn probability with increasing distance from treated areas (Figure 6). However, by 2037 the modeled burn probabilities exceeded those of the pretreatment scenario across the study area (Figures 5 and 6)

Mean conditional burn probabilities (flame lengths >2 m) for the NoTrt scenario declined slightly from 2007 to 2017 and from 2017 to 2027 but increased substantially in 2037 (Figure 7). Each of the three diameter-limited thinning scenarios resulted in considerable reductions in mean conditional burn probability for 2017 and 2027 and were all nearly indistinguishable from each other, regardless of simulation year. Although mean burn probabilities for the three treatment scenarios increased in 2037, all three scenarios were below that of the NoTrt scenario in 2037 (Figure 7).

Discussion

Simulated Stand-Level Treatments

All forest dynamics simulations were done in the absence of unplanned disturbances, namely wildland fire and insect outbreaks. Given the 30-year simulation period, this may or may not be a reasonable assumption; however this assumption was necessary to attain meaningful comparisons among treatment scenarios. The modeled stand structural changes for the first cycle after treatment implementation (i.e., reduced tree density, basal area, canopy cover, and canopy bulk density and increased canopy base height) were similar to those reported in studies of actual fuel reduction treatments (Stephens and Moghaddas 2005, Schmidt et al. 2008, Harrod et al. 2009, Stephens et al. 2009) and are consistent with reduced crown fire potential (Agee and Skinner 2005). With the exception of canopy base heights, the persistence of these structural changes relative to that for no treatment demonstrates a fairly long-lived effect associated with a single-entry fuel treatment (Figures 3 and 4).

The initial increases in canopy base heights within thinning and prescribed fire stands are a product of removing trees from the understory and midcanopy layers either by thinning or burning. However, the finding that the most conservative thinning treatment (30.5 cm or 12 in. dbh limit) resulted in only a slight increase in canopy base height indicates that 7–10 years after treatment limiting thinning to this extent may not effectively reduce ladder fuels. North et al. (2009) argue that thinning trees above the 25 to 40.6 cm dbh (10 to 16 in.) class is not necessary for reducing ladder fuels. The modest increase in canopy base heights as the thinning dbh limit increases from 50.8 cm (20 in.) to 76.2 cm (30 in.) suggests there may be little justification for thinning trees larger than 50.8 cm (20 in.) dbh to

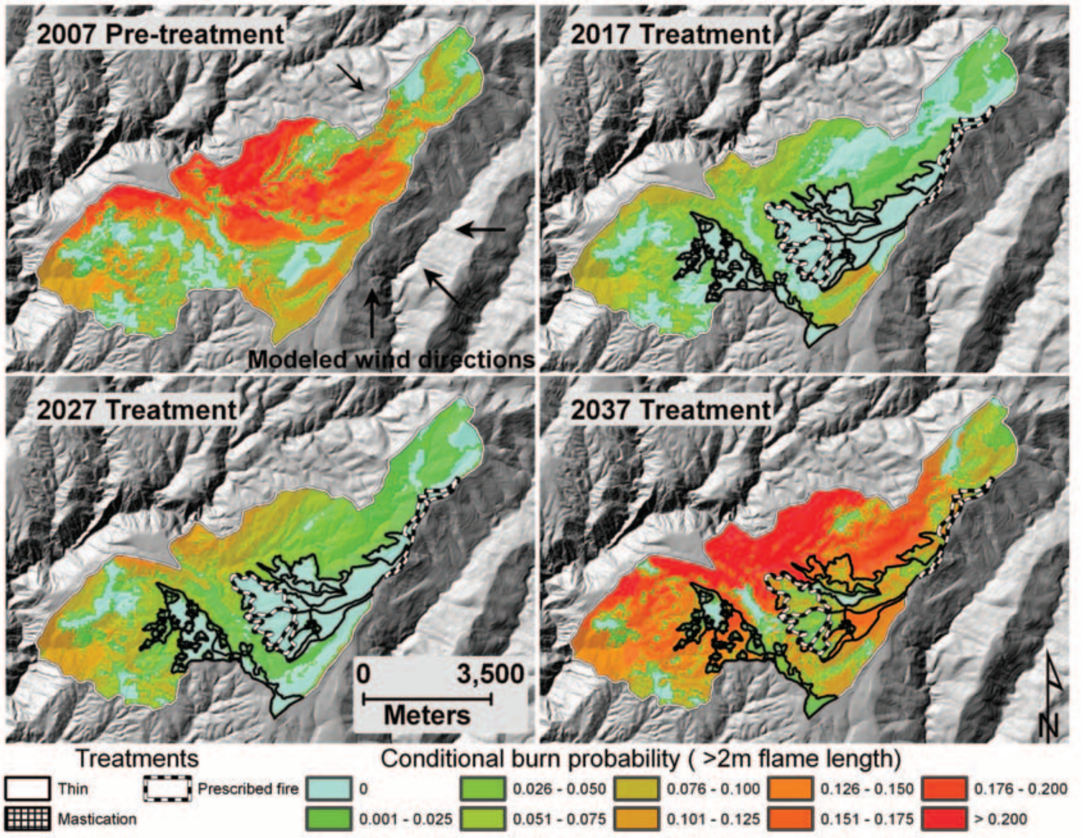

Figure 5. Conditional burn probabilities across the Last Chance landscape for which simulated flame lengths are greater than 2 m. Burn probabilities are reported for the pretreatment conditions (2007), as well as for the treated (76.2 dbh limit) scenarios modeled 30 years from pretreatment. Probabilities are based on 5000 randomly placed ignitions simulated using RANDIG (see Methods for explanation). Treatment types and boundaries along with modeled wind directions are also displayed.

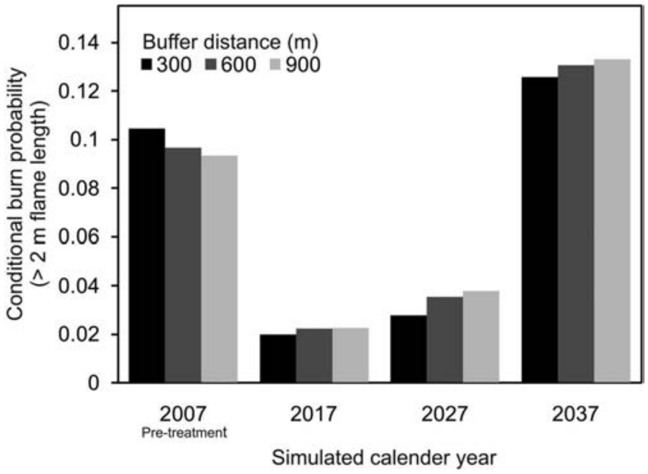

Figure 6. Mean conditional burn probabilities (simulated flame lengths >2 m) within concentric, nonoverlapping buffers immediately surrounding treated areas in the Last Chance core study area. Means are reported for the pretreatment conditions (2007), as well as for the treated (76.2 dbh limit) scenarios modeled 30 years from pretreatment. Probabilities are based on 5,000 randomly placed ignitions simulated using RANDIG (see Methods for explanation).

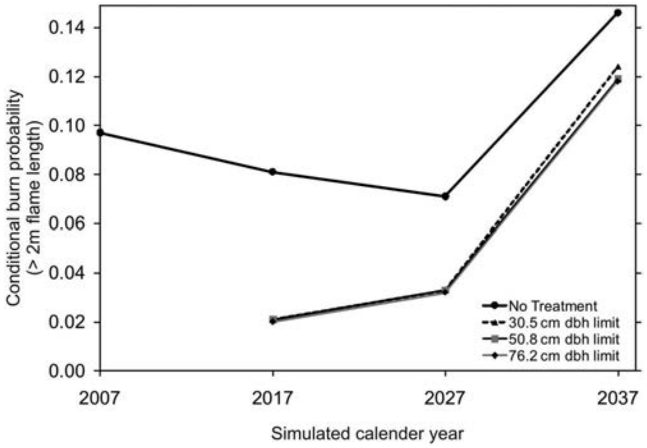

Figure 7. Mean conditional burn probabilities across the Last Chance landscape for which simulated flame lengths are >2 m. Three diameter-limited thinning scenarios along with a no treatment scenario are reported. Each scenario was modeled into the future based on output from the Forest Vegetation Simulator, using our 2007 field inventory plot data as a baseline. Probabilities are based on 5,000 randomly placed ignitions simulated using RANDIG (see Methods for explanation). Note that the three thinning scenarios are nearly indistinguishable, with the exception of a slight departure for the 30.5-cm scenario in 2037.

reduce potential fire behavior in forests similar to those studied here.

As regeneration after treatment disturbances takes place, the established trees begin to grow into the understory canopy layer, resulting in decreased canopy base heights over time (2027 and 2037 in Figures 3 and 4). In 2027 only prescribed fire stands exhibited higher canopy base heights relative to no treatment. This is probably due to a substantial pruning effect (i.e., high scorch heights) brought about by a fairly aggressive burning prescription and is evident from the almost 6-m average canopy base heights and substantial reductions in tree density within burned stands for 2017 and 2027. The much lower canopy base height for the 76.2 cm (30 in.) dbh thinning scenario in 2027 is likely due to the regeneration response to increased growing space created by the more intensive disturbance, i.e., lower residual canopy cover and tree density.

As with most modeling exercises, results are inherently subject to a certain number of assumptions and ideas put forth by the modeler (Collins et al. 2010). This is especially the case for canopy base height estimates over time from FVS, namely in 2027 and 2037 (Figures 3 and 4). In the absence of pertinent local data we made assumptions in modeling seedling establishment based on local expert knowledge and on our own familiarity with the study site. The modeled number of established trees varied by species and involved stochasticity among stands and among FVS cycles. Although these assumptions are somewhat subjective, we believe our modeled forest stand dynamics reflect reasonable progressions of treated and untreated stands.

Simulated Landscape-Level Fire Spread

One of the primary objectives of a landscape fuel treatment project is to reduce the potential for exacerbated fire effects, not only within treated areas but also across the landscape (Weatherspoon and Skinner 1996, Finney 2001). Inasmuch as the modeled burn probabilities we present (>2-m flame lengths) can serve as a proxy for more damaging or problematic fire occurrence, the reduced conditional burn probabilities across the Last Chance study area after simulated treatments indicate an effective landscape fuel treatment project (Figure 5). This reduction in burn probabilities was evident well outside of treatment boundaries and persisted for almost 20 years after simulated treatments (Figure 6). Limiting our analyses to only those probabilities in which flame lengths were >2 m was an attempt to separating out higher intensity modeled fire behavior, which presumably is associated with exacerbated fire effects (fires with flame lengths <2 m would be mostly beneficial to this ecosystem). Furthermore, when fires are modeled for a fixed period of time, increased burn probabilities are indicative of faster spread rates (Finney et al. 2007, Seli et al. 2008). Faster spread rates in many forested fuel types are related to higher fireline intensities (Albini 1976), which can lead to increased fire effects. This assumption would not necessarily be valid when surface fuels are dominated by grasses (van Wagtendonk 1996). However, because we did not have grass or timber-grass fuel models in the Last Chance study area either pre- or post-treatment we believe that burn probabilities are reasonable indicators of potential fire effects.

The treatment effectiveness across the entire Last Chance landscape exists in the absence of a dispersed or regular arrangement of treated stands. We hypothesize that a few factors related to the position and size of the individual treatment units contributed to the modeled reductions in burn probabilities. Although there are several individual treated stands with, in some cases, differing prescriptions, the Last Chance treatments primarily consist of two large blocks (Figure 5). These treatment blocks are centered about the long axis of the study area (Figure 5). We suggest that because of the approximate centralized position of the treatments, many of the modeled fires intersected one or both of the treatment blocks. In addition, the large size of the treatment blocks may have increased the potential to slow fire spread. The centralized location may have also been a safeguard against fires becoming too large, given that the simulated fires burned under multiple wind directions using RANDIG (Table 2). If treatments were positioned toward one end of the study area or more dispersed throughout the study area the varying wind directions among simulated fires may have had led to more fires either avoiding treated areas or overwhelming treatments. Addressing these hypotheses more directly would involve substantial theoretical modeling that exceeds our intent of analyzing an actual landscape fuel treatment project.

The lack of clear differences among diameter-limited thinning scenarios for landscape-level burn probabilities (Figure 7) bears some attention. It is possible that the generally open forest structure pretreatment (2007 in Figures 3 and 4) has some impact. Because initial canopy cover estimates averaged near 50%, there may not have been much difference among the thinning scenarios, which aimed to reduce canopy cover to between 40 and 60%, depending on the scenario. The low canopy cover for the Last Chance study area is due in part to the history of extensive timber operations in the area (K. Jones, Tahoe National Forest, pers. comm., Jul. 29, 2008).

Another likely explanation for lack of differences among diameter-limited thinning scenarios lies in our surface fuel assumptions for the thinning treatments. In our modeling, treatment of surface fuels after thinning (i.e., pile and burn) did not change among diameter-limited scenarios, and thus surface fuel model assignments were unchanged among thinning scenarios for the first two cycles after thinning (2017 and 2027) (Table 1). As a result, the similarity in landscape-level conditional burn probabilities among the three scenarios is not too surprising, at least in the first two FVS cycles. We submit that our supposition that residual surface fuels would not vary much among diameter-limited thinning scenarios is reasonable, assuming that funding treatment of activity fuels and natural surface fuels after thinning is independent of the revenues from the thinning. One potential difference, however, is that the most conservative diameter-limited scenario (30.5 cm or 12 in.), which leaves more trees (Figure 3), may result in more restricted access throughout the stand. If activity fuels and natural surface fuels are piled mechanically, then this restricted access could limit the amount of woody fuel actually removed from the stand, which could result in increased potential for higher intensity surface fire and reduced treatment effectiveness.

Stand development within both treated and untreated stands probably drove the observed increases in conditional burn probabilities across the Last Chance study area over time (Figures 5–7). However, these increases in burn probabilities (>2-m flame lengths) were not constant over our simulation duration. The increase in mean conditional burn probability from 2017 to 2027 was well below that from 2027 to 2037 for the treatment scenario (Figure 7). This result suggests landscape-level treatment longevity of approximately 20 years based on a single-entry treatment. Although we do not model it, maintenance treatments (e.g., prescribed fire) would probably extend this longevity across the landscape. Recall that we simulated thinning, burning, and mastication treatments in the 1st year of the first FVS cycle (2007). Results from Finney et al. (2007) indicating reductions in mean burn probabilities at treatment rates of 1% per year (20% of the landscape every 20 years) support our findings. (Last Chance treatments covered 25% of the study area.)

Modeling Limitations

One of the obvious limitations to our analysis is the lack of consistency in vegetation and fuel layers between the core study area and the buffer area (Figure 1). Both the different sources of the data and the static nature of the buffer layer may have led to anomalous fire behavior near the edges of the core area. However, there is little evidence for such abnormality when burn probabilities are displayed geographically (Figure 5). Because the vegetation and fuel layers for the core study area were derived from an intensive inventory consisting of almost 200 field plots, increasing the field sampling to include data collection for a buffered area would have required substantial additional effort. Given limited budgets, a better strategy may have been to sample a larger buffered area less intensively and forego the detail gained by more closely spaced inventory plots.

It is likely that the fuel model selection logic we developed (Figure 2; Table 1) had an impact on conditional burn probability outputs over the simulated duration. Our assumptions that thin/pile and burn stands progressed from moderate-load conifer litter to high-load conifer litter surface fuel models and, by the final cycle, entered into the untreated selection logic may or may not represent realistic fuel recovery. Little work has been done in the area of fuel model succession. Miller and Davis (2009) developed a dynamic model of fuel succession after fire, in which transitions from one fuel model to the next were based on both fire severity and time since fire. These transitions and rates were based on expert opinion and follow logic similar to ours with respect to time since disturbance. More empirical studies of fuel recovery after disturbance are needed to form robust methodologies for dynamically assigning fuel models in long-term simulation studies.

Another limitation of our analysis is that the conditional burn probabilities we report are different from actual burn probabilities for our study area. The probabilities we report are "conditional" on the occurrence of an ignition within the larger buffered study area, under the modeled moisture and wind conditions. Based on analysis of actual fires within and around the larger buffered study area, fire rotations were between 214 and 227 years, depending on the length of the reporting period (1950–2008 or 1900–2008, respectively), which translates to an approximately 0.004 annual probability of the entire study area being burned, substantially less than our average conditional burn probability (>2 m flame lengths) for the NoTrt scenario in 2007 of 0.097. Despite this discrepancy, the probabilities we report are a robust and useful measure of fuel treatment effects across landscapes (Ager et al. 2010).

Ultimately there is no substitute for learning from actual wildland fires affecting completed fuel treatments. Although there is a suite of case studies demonstrating stand-level fuel treatment performance in wildland fires (e.g., Martinson and Omi 2002, Finney et al. 2003, 2005, Raymond and Peterson 2005, Skinner et al. 2005, Moghaddas and Craggs 2007, Ritchie et al. 2007, Strom and Fulé 2007, Safford et al. 2009), there are very few studies that have analyzed performance of coordinated landscape fuel treatments in an actual wildland fire (see Finney et al. 2005). The probability of such an opportunity occurring is low given the current rarity of implemented landscape fuel treatments (Collins et al. 2010). As a result, much of the analysis of landscape fuel treatments is largely based on modeling, which is subject to the limitations we have discussed throughout.

Conclusions

It is clear from our findings that although the Last Chance project does not use the dispersed, regular arrangement of treatments (see Finney 2001) or a more intensive modeling effort to spatially locate treatment (see Finney 2007), the landscape fuel treatment effort demonstrates effective reduction in modeled burn probabilities. Because our analysis incorporates variable wind directions and speeds, one of the dominant drivers of fire spread, we believe these results reflect a realistic assessment of treatment effectiveness and not simply results driven by a few key modeling assumptions. These winds represent actual conditions that are associated with large fire potential within the Last Chance study area. Furthermore, we used detailed and extensive forest stand structure data as inputs for our fire and forest dynamics modeling. These factors, along with the modeling adaptations we incorporated (modified fuel model selection and stochastic regeneration) contribute to a robust analysis, despite the limitations we discussed.

Although there were differences in residual forest structure among diameter-limited thinning scenarios at the stand level, the lack of clear differences in >2 m flame length burn probabilities among thinning scenarios suggests that at the landscape scale effective fuel reduction treatments rely more on treating surface fuels and thinning ladder fuels than on thinning diameter limits. However, it is worth noting that our modeling may under represent crown fire propagation and spotting and thus may not be able to capture differences in reduction of crown fire potential among thinning scenarios. As Safford et al. (2009) demonstrated, fuel treatments in actual wildland fire areas thinned at lower intensities (e.g., hand-thinning) resulted in little to no reduction in fire severity, whereas in areas more intensively thinned fire severity was substantially reduced within 50 m of treatment boundaries. Capturing these changes in fire intensity and subsequent effects via modeling (e.g., a probabilistic reduction of propagating crown fire, spotting) after landscape fuel treatment implementation would improve our ability to evaluate whether or not a landscape fuel treatment achieved such objectives.

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Population Ecology

Realized Population Change for Long-Term Monitoring: California Spotted Owl Case Study

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ABSTRACT The annual rate of population change (λ_t) is a good metric for evaluating population performance because it summarizes survival and recruitment rates and can be used for open populations. Another measure of population performance, realized population change (Δ_t) is an encompassing metric of population trend over a period of time; it is the ratio of population size at an end time period relative to the initial population size. Our first goal was to compare mean λ and Δ_t as summaries of population change over time. Our second goal was to evaluate different methods for estimating these parameters; specifically we wished to compare the value of estimates from fixed effects models, random effects estimates from mixed effects models, and Bayesian Markov chain Monte Carlo (MCMC) methods. Our final goal was to evaluate the use of the posterior distribution of Δ_t as a means for estimating the probability of population decline retrospectively. To meet these goals, we used California spotted owl (*Strix occidentalis occidentalis*) data collected on 3 study areas from 1990 to 2011 as a case study. The estimated MCMC median λs for 2 of the study areas were 0.986 and 0.993, indicating declining populations, whereas median λ was 1.014 for the third study area, indicating an increasing population. For 2 of the study areas, estimated MCMC median Δ_ts over the 18-year monitoring period were 0.78 and 0.89, suggesting 21% and 11% declines in population size, whereas the third study area was 1.22 suggesting a 22% increase. Results from Δ_t analyses highlight that small differences in mean λ from 1.0 (stationary) can result in large differences in population size over a longer time period; these temporal effects are better depicted by Δ_t. Fixed effects, random effects, and MCMC estimates of mean and median λ and of Δ_t were similar ($\leq$9% relative difference). The estimate of temporal process variance was larger for MCMC than the random effects estimates. Results from a Bayesian approach using MCMC simulations indicated that the probabilities of a $\geq$15% decline over 18 years were 0.69, 0.40, and 0.04 for the 3 study areas, whereas the probabilities the populations were stationary or increasing were 0.07, 0.22, and 0.82. For retrospective analyses of monitored populations, using Bayesian MCMC methods to generate a posterior distribution of Δ_t is a valuable conservation and management tool for robustly estimating probabilities of specified declines of interest. © 2013 The Wildlife Society.

KEY WORDS Bayesian MCMC approach, California, California spotted owl, hierarchical model monitoring, Pradel's temporal symmetry model, random effects estimator, rate of population change, realized population change, *Strix occidentalis occidentalis*.

Long-term monitoring programs are often focused on species of concern, from game to threatened species. Management of these species is often controversial and sociopolitical challenges are often as important as biological ones. Controversial species require clear, simple, and objective biological metrics to inform the management decision process, particularly for regular and relatively short-term intervals, such as management plans and status updates (e.g., $\leq$5 years). Population size is often used because of its ease of interpretation and because management or conservation goals often include maintaining population levels close to sustainable objectives (Thompson et al. 1998, Williams et al. 2002) or above some minimum threshold, such as the size of a minimum viable population (Soulé 1980). However, population size alone reveals little about the long-term

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sustainability of a population (Lancia et al. 2005). Determining whether the population is increasing, decreasing, or remaining stable is also critical to ensuring future population size objectives (Thompson et al. 1998, White et al. 2002, Williams et al. 2002). The annual rate of population change (λ_t) is a good metric for evaluating population performance because it summarizes survival and recruitment rates and can be used for open populations (Nichols and Hines 2002). The value of λ_t is interpreted as the rate of annual (or other time period of interest) increase or decrease in the population, and is used more frequently for monitoring and management decisions.

Another metric used for evaluating changes in population status is realized population change (Δ_t), which is the change in population over a period of time (Franklin et al. 2004). This quantity is the ratio of population size at some point in time period K, relative to the initial population size N ($\Delta_t = N_K/N$), which reflects the cumulative effect of λ_t for a time period of interest. For example, if λ_t had a geometric mean of 0.97, a population size starting at 100 would decline to approximately 86 over 5 years (a common management time frame) and Δ_t would be 0.86. Specifically, Δ_t incorporates all estimates of λ_t and provides an intuitive number for evaluating population change over periods of time.

In the past, the confidence intervals (CI) for estimates of mean λ and of Δ_t were used to evaluate population decline. That is, if the CI included 1, even if just barely, the conclusion was that there was no evidence for a decline. However, with this methodology, the influence and probability of a Type II error (inability to detect a decline or change) cannot be eliminated from the interpretation of no decline. The key element missing in this approach was the ability to estimate the probability of decline. Using Bayesian Markov chain Monte Carlo (MCMC) methods, a posterior distribution of Δ_t can be used to estimate any probability of decline. The approach has not been widely used, although Gerrodette and Rojas-Bracho (2011) used it to evaluate declines in vaquita (*Phocena sinus*) over a 15-year monitoring period. Indeed, the posterior distribution of Δ_t provides a robust method for detecting and describing retrospective population trajectories, similar to how population viability analysis (PVA) and more generally, projection models, are used to evaluate potential prospective population trajectories.

The inclusion of sampling variation in estimates of λ_t can negatively bias estimates of Δ_t, similar to how it can negatively bias estimates of persistence in PVA models. Bayesian MCMC methods can be used to separate process variation from sampling variation during the estimation of Δ_t. In addition to Bayesian MCMC methods, a random effects estimator, also called a shrinkage or empirical Bayes estimator, is an analytical approach to separate sampling variation from the overall process variance (Efron and Morris 1977, Ver Hoef 1996, Burnham and White 2002). Depending on computing tools available, both approaches can be used for estimating λ_t and Δ_t.

Our first goal was to compare mean λ and Δ_t as summaries of population change over time. Our second goal was to evaluate different methods for estimating mean λ and Δ_t. Specifically, we wished to compare the value of estimates based on a random effects estimator from a mixed effects model and a Bayesian MCMC approach for evaluating population performance of species with long-term monitoring data. Our final goal was to evaluate a Bayesian approach to generate a posterior distribution of Δ_t as a means to estimate the probability of population decline retrospectively. We use data collected on the California spotted owl (*Strix occidentalis occidentalis*) as a case study. The California spotted owl remains a focal species of conservation concern, and knowledge of population trends is an important component of assessing status and informing forest management planning efforts.

STUDY AREA

We used data from spotted owls on 3 study areas in the Sierra Nevada and southern Cascade Mountains, California, collected from 1990 to 2011 (Fig. 1). Although we did not randomly select the study areas, they spanned the length of the contiguous California spotted owl range in the Sierra Nevada and encompassed all habitat types known to be used by spotted owls in the Sierra Nevada. The Lassen (LAS) study area was in the southern Cascades, but it was included in the Sierra Nevada province by the United States Forest Service for management purposes (U.S. Forest Service 2004). Most of the LAS and Sierra (SIE) study areas were located on public land managed by the United States Forest Service, whereas the Sequoia and Kings Canyon (SKC) study area was in 2 national parks. Franklin et al. (2004) and Blakesley et al. (2010) described in detail the LAS, SIE, and SKC study areas; however, SKC has changed from Blakesley et al. (2010). In 2006, the study area for SKC was reduced; all estimates of λ_t were based on data from this reduced study area. Long-term mark-resight data were available for each study population. The number of marked birds varied each year, but generally ranged between 40 and 90, with 4–14 new birds marked each year (Table 1).

METHODS

Field Surveys

Field methods for the study of spotted owl population dynamics have been well described elsewhere (Forsman 1983; Franklin et al. 1996, 2004; Anthony et al. 2006). In particular, the field methods and protocols used to collect the data are detailed by Franklin et al. (2004). Therefore, we present only a brief summary of the methods used to capture and recapture (by resighting) owls.

We conducted surveys to find and locate California spotted owls from 1 April to 31 August on LAS and from 1 March to 30 September on SIE and SKC. We identified owls by capturing and banding, or by resighting owls previously banded with unique color band combinations. We surveyed spotted owls primarily at night by vocally imitating spotted owl calls or by broadcasting recordings of spotted owl calls. We completely surveyed the core study areas on ≥ 3 occasions throughout each field season. When we detected owls, we

Figure 1. Outline of southern Cascade and Sierra Nevada Mountains, California, showing the location of 3 study areas for California spotted owls, 1990–2011.

conducted walk-in surveys during daylight hours to visually locate owls, identify color bands, or capture unbanded owls.

We identified spotted owls to sex (male, female) by vocalization and behavior, and determined age by plumage characters (Franklin et al. 1996). Owls can be identified to 4 age classes (juvenile [young of the year], 2 subadult ages [1–2 years old; 2–3 years old], and adult [≥3 years old]; Moen et al. 1991). We use the term non-juvenile owl to refer to subadult and adult age classes; we used only non-juvenile owls for our analyses.

Rate of Population Change

We used each owl's encounter history to estimate the annual rate of population change in territorial owls (λ_t) using Pradel's temporal symmetry model (Pradel 1996, Nichols and Hines 2002, Franklin et al. 2004) in Program MARK (White and Burnham 1999). We refer to Pradel's temporal symmetry model as the Pradel model. All 3 study areas had territorial survey areas, in which some areas were not consistently surveyed, and a subset core study area, which was surveyed consistently for estimation of λ_t. In the core areas, coverage was complete, in that each year, we surveyed areas without known owl territories, as well as areas with known owl territories. For population growth rate to represent changes in the number of owls for the Pradel model, the study area size and boundary must remain unchanged through time (Hines and Nichols 2002, Franklin et al. 2004). Consequently, we used data only from the core areas to interpret λ_t as the annual rate of population change.

We used the ($\phi\lambda p$) structure of the Pradel model, where ϕ is apparent survival (probability that an owl alive in year t survived to the next year $t + 1$ and remained on the study area [i.e., available for recapture or resight]) and p is the resight (by recapture or resight) probability. Based on previous California spotted owl analyses (Franklin et al. 2004, Blakesley et al. 2010), we used a model with fixed effects of sex and year, $\lambda(t)\phi(t)p(s \times t)$, where s = sex and t = year as a categorical time effect. For each study area, we estimated the overdispersion parameter ($\hat{c}$) using the median $\hat{c}$ procedure in Program MARK under the Cormack-Jolly-Seber (CJS) global model $\phi(s \times t)p(s \times \mathrm{t})$. When $\hat{c}$ was >1, we used $\hat{c}$ to inflate variances of parameter estimates (Burnham and Anderson 2002).

Using the model structure above, $\lambda(t)\ \phi(t)\ p(s \times t)$, we estimated the mean rate of population change using a fixed effect model ($\bar{\hat{\lambda}}$). Using the same model, we also used a mixed model approach to estimate the mean rate of population change ($\bar{\tilde{\lambda}}$) and its temporal process variation ($\hat{\sigma}^2$), as well as to generate random effects estimates of λ_t ($\tilde{\lambda}_t$; White et al. 2001). The parameters ϕ and p were fixed effects and λ_t was a random effect. To estimate $\bar{\tilde{\lambda}}$, we used an intercept-only (means) model for λ_t. We did not include the first 2 estimates and last estimate of λ_t to estimate mean λ because the first and last estimates were confounded with estimation of p, and the second estimate has a potential bias from trap response or a learning curve experienced by field crews at the beginning of the studies (Hines and Nichols 2002). We calculated $\bar{\hat{\lambda}}$, SE($\bar{\hat{\lambda}}$), $\bar{\tilde{\lambda}}$, SE($\bar{\tilde{\lambda}}$), and $\hat{\sigma}^2$ on the log scale and used the delta method to estimate variance of the back-transformed geometric means of $\hat{\lambda}$ and $\tilde{\lambda}$ (Franklin et al. 2004). We used the log-scale because the geometric mean generates an unbiased estimate of mean λ over a finite time period, whereas the arithmetic mean generates a biased estimate (Morris and Doak 2002).

Table 1. Descriptions of the 3 study areas in the southern Cascades and Sierra Nevada, California, and sample sizes of California spotted owls.

Study area[a]	Years	Area (km^2)	Avg. total no. marked[b]	Avg. new marked/year[c]
LAS	1990–2011	1,254	88	14
SIE	1990–2011	562	76	8
SKC	1991–2011	182	59	7

[a] LAS is Lassen, SIE is Sierra, and SKC is Sequoia Kings Canyon.

[b] Average number of marked owls on study area; includes territorial adult and subadult owls.

[c] Average number of newly marked owls on study area; includes territorial adult and subadult owls.

Both LAS and SIE had expansion areas, areas in which surveying began several years after the start of the study. If these were not accounted for, new owls found in these areas would enter the Pradel model as new recruits, and result in a positive bias in estimates of λ_t. Therefore, we accounted for these areas by grouping them separately and excluding estimates of λ_t from the year of and year following the expansion, and estimates of p for the year of expansion (see Blakesley et al. 2010, Appendix G, for a detailed explanation of the procedure). One study area, SKC, had a year of missed data collection (2005); we used an unequal time interval to account for this in Program MARK, which resulted in an average survival over the 2-year interval. We did not use the average estimate from these 2 years (2004–2005 and 2005–2006) in any random effects analyses because random effects in Program MARK assumes equal time intervals.

Realized Population Change

We translated fixed effects estimates of $\lambda_t (\hat{\lambda}_t)$ into estimates of realized population change ($\hat{\Delta}_t$) on each study area, which is the proportional change in estimated population size, relative to the initial population size (Franklin et al. 2004). We calculated $\hat{\Delta}_t$ as the product $1 \times \hat{\lambda}_k \times \hat{\lambda}_{k+1} \times \hat{\lambda}_{k+2} \times \cdots \times \hat{\lambda}_K$, where k was year of the first estimated λ_t (i.e., the third year because the first 2 estimates of λ_t were confounded or biased) and K was the last (i.e., the second to last estimate because the last estimate was confounded). For each study area, we used the delta method to estimate variance of realized change (on the natural log scale) and the associated back-transformed CIs (Franklin et al. 2004). We also used the random effects estimates of $\lambda_t (\tilde{\lambda}_t)$ to estimate realized population change ($\tilde{\Delta}_t$). Because the random effects variance estimate is conditionally biased, we based CIs on root mean square error (RMSE; White et al. 2001, Burnham and White 2002), which includes a term for the difference between $\tilde{\Delta}_t$ and $\hat{\Delta}_t$ (e.g., $[\tilde{\Delta}_t - \hat{\Delta}_t]^2$). To estimate the covariance between random effects estimates, we multiplied the correlations between fixed effects estimates by the RMSE^2 (i.e., variance) of each estimate.

To estimate probabilities of population declines or increases for each area, we used a bayesian approach via MCMC sampling implemented in Program MARK to estimate posterior distributions of λ_t ($\lambda_{t\ \mathrm{MCMC}}$) using the same mixed effects model and years as described above. We used the posterior distributions of $\lambda_{t\ \mathrm{MCMC}}$ to estimate the posterior distribution of median λ (λ_{MCMC}) and Δ_t ($\Delta_{t\ \mathrm{MCMC}}$). For all MCMC simulations, we used 4,000 tuning samples, 1,000 burn in samples, and 20,000 realizations. We used vague priors for all parameters included in the model. For estimating median λ_{MCMC} and $\Delta_{t\ \mathrm{MCMC}}$, we used a hyperprior for μ and σ of λ_t. For μ, we used a normally distributed prior with mean $= 0$ and standard deviation $= 100$ and for σ, we used a gamma prior to model its transformation, $1/\sigma^2$, with $\alpha = 1.00001$ and $\beta = 0.000001$. Although we did not use estimates of ϕ and p in the hyperprior to estimate μ and σ of λ_t, we did include them in the model, $\lambda(t)\phi(t)p(s \times t)$, and they required a prior distribution. Because they were logit transformed parameters, we used a normal prior distribution with mean of 0 and a standard deviation of 1.75, which is a vague prior when back transformed to the real scale (2.5th and 97.5th percentiles of approximately 0.02 and 0.98, with a uniform distribution between those percentiles). We determined if the Markov chains converged using the Gelman–Rubin statistic, R-hat (Gelman et al. 2004). For each parameter, we used 10 chains of 1,000 each and used a threshold of R-hat < 1.1 to indicate adequate sampling of the posterior distribution.

RESULTS

We used encounter histories for 323, 317, and 165 individual owls, for LAS, SIE, and SKC respectively, to model rate of population change. Median $\hat{c}$ ranged from 1.09 to 1.18, suggesting some overdispersion but no serious lack of fit. We adjusted all variance estimates by site-specific estimates of c. The MCMC chains for all model parameters converged (R-hat < 1.1).

Estimates of mean $\hat{\lambda}$, $\tilde{\lambda}$, and median λ_{MCMC} were $<$1.0 for LAS and SIE, which suggested declining populations (Table 2). Estimates of median λ_{MCMC} were very close to $\hat{\bar{\lambda}}$ and $\tilde{\bar{\lambda}}$, although estimates of σ were $\geq$2.9× greater for MCMC than for the random effects estimate (Table 2).

Table 2. Estimates of mean annual rate of population change ($\bar{\lambda}$) and its temporal process standard deviation ($\hat{\sigma}$). Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Random effect estimates are based on mixed effects models using a means model for time-specific estimates of rate of population change (λ; random effect) with fixed effects for time-specific apparent survival (ϕ) and resight probability (p), and Markov chain Monte Carlo (MCMC) estimates are based on a Bayesian approach to generate posterior distributions of annual rate of population change (λ_t) that is implemented in Program MARK.

Study area	Estimator[a]	$\bar{\lambda}$[b]	SE	95% CI		$\hat{\sigma}$	95% CI	
LAS	FE	0.985	0.017	0.950	1.022			
	RE	0.987	0.011	0.967	1.008	0.018	0.013	0.026
	MCMC[c]	0.986		0.880	1.072	0.052	0.012	0.212
SIE	FE	0.993	0.017	0.959	1.027			
	RE	0.990	0.009	0.973	1.008	0.000	0.000	0.052
	MCMC	0.993		0.925	1.058	0.037	0.011	0.134
SKC	FE	1.016	0.021	0.976	1.057			
	RE	1.010	0.014	0.982	1.038	0.018	0.000	0.101
	MCMC	1.014		0.907	1.170	0.058	0.015	0.217

[a] FE are fixed effects estimates, RE are random effects estimates from a mixed effects model, and MCMC are estimates from 20,000 simulations.

[b] This estimate does not include the first 2 estimates and last estimate of λ_t because they were confounded or potentially biased.

[c] MCMC estimates are the median and 2.5 and 97.5 percentiles from the posterior distribution, based on 20,000 simulations.

For LAS and SKC, the annual pattern of λ_t was the same between the fixed effects, random effects, and MCMC estimates, although values of $\tilde{\lambda}_t$ and $\lambda_{t\ \mathrm{MCMC}}$ were closer to their estimated means compared to $\hat{\lambda}_t$ (Fig. 2). On average, the variance was greater for fixed effects estimates (Fig. 2a) than for random effects estimates from the mixed model (Fig. 2b). However, because we used RMSE for the random effects estimates, the variance for several estimates of $\tilde{\lambda}_t$ was greater than for the fixed effects $\hat{\lambda}_t$ (most noticeably, SIE 1992 and 1997 and SKC 1992, 2001, and 2002). The MCMC estimates of median $\lambda_{t\ \mathrm{MCMC}}$ had smaller credible intervals than fixed effects CIs (Fig. 2a,c), and although some credible intervals were larger than the random effects CIs, they were more consistent (Fig. 2b,c).

The consecutive estimates of Δ_t reflected the temporal variation in λ_t, with $\tilde{\Delta}_t$ (Fig. 3b) not necessarily having less variance than $\hat{\Delta}_t$ (Fig. 3a and Table 3). Credible intervals of estimates of median $\Delta_{t\ \mathrm{MCMC}}$ (Fig. 3c) started out smaller than CIs of $\hat{\Delta}_t$ (Fig. 3a), but grew to be approximately the same size by the end of the monitoring period. Over the 18-year study period, the different estimators of Δ_t indicated population declines of 21–22% for LAS and 11–16% for SIE, and an increase of 16–27% for SKC, although CIs overlapped 1.0 for all estimators and study areas (Fig. 3 and Table 3). We found small but variable differences in magnitude between the estimators of Δ_t (1–9% absolute difference; Table 3). The size of standard errors for Δ_t were also variable with no particular pattern between the estimators (Table 3).

From the Bayesian approach, posterior distributions of $\Delta_{t\ \mathrm{MCMC}}$ showed the 3 populations had different population trajectories (Fig. 4). The probability that any population declined by ≥30% was low, varying from 0.24 for LAS to <0.01% for SKC (Table 4). The probability of a minor decline was more substantial; we calculated a 0.69 and 0.40 probability LAS and SIE declined by ≥15% (Table 4). The populations had variable probabilities of remaining stationary or increasing as well; SKC had a relatively high probability (0.82), whereas LAS and SIE had lower probabilities (0.07 and 0.22; Table 4).

DISCUSSION

For long-term monitoring data, Δ_t is an insightful metric for portraying the cumulative dynamics of a population across

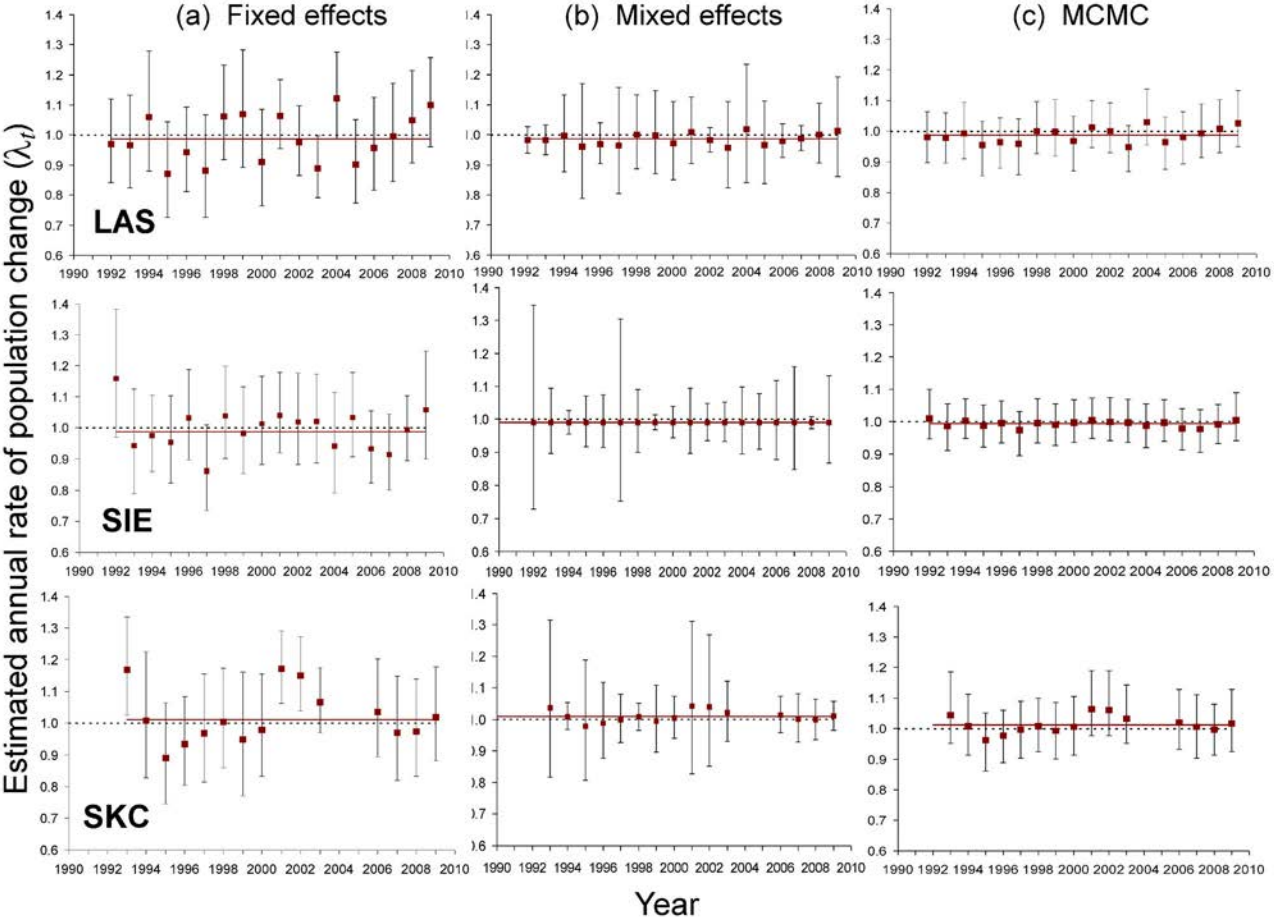

Figure 2. Estimates of annual rate of population change (λ_t) and 95% confidence intervals based on (a) fixed effects estimates, (b) random effects estimates from a mixed effects model, and (c) a Bayesian Markov chain Monte Carlo (MCMC) approach for California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. Solid lines indicate the best estimates of mean λ from a mixed effects model for each study area. We used the root means squared error for 95% confidence intervals for random effects estimates, and show the median and 2.5 and 97.5 percentiles for MCMC methods.

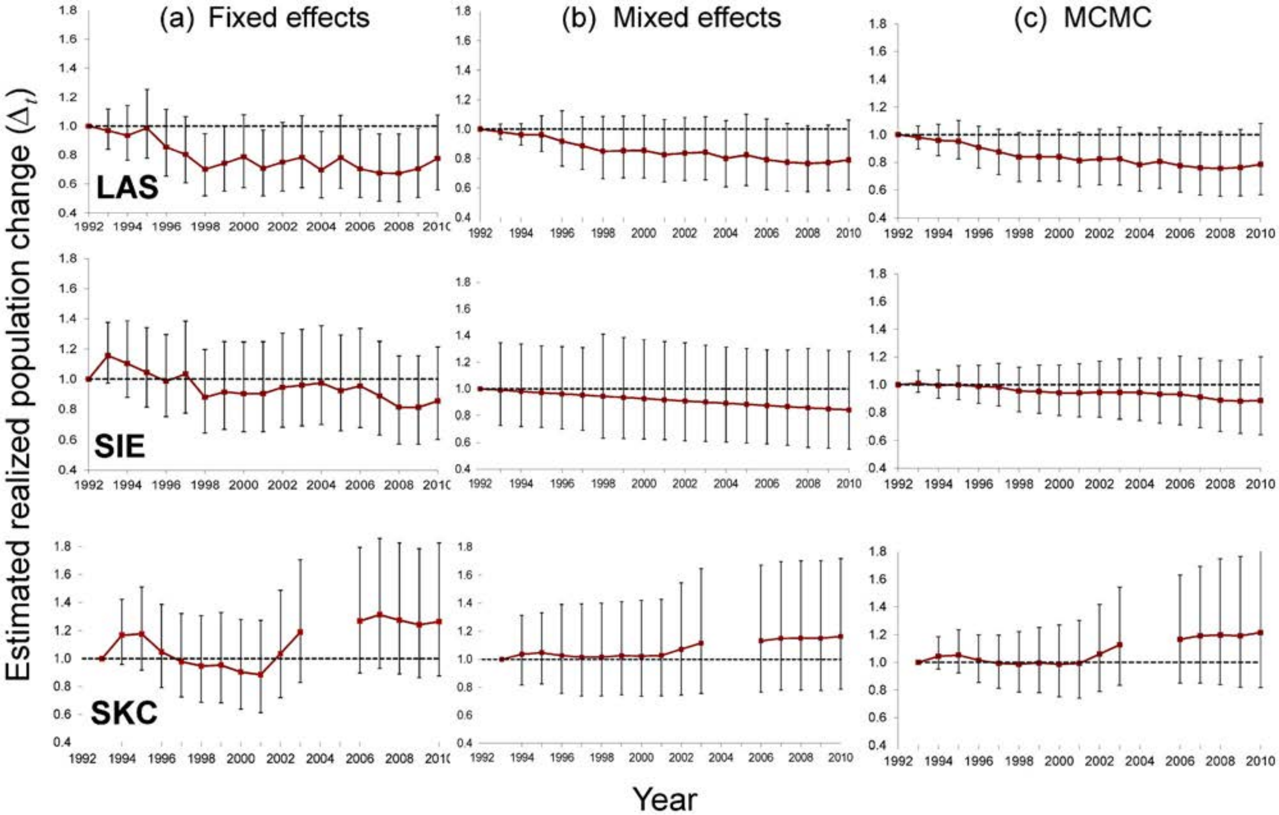

Figure 3. Estimates of realized population change (Δ_t) and 95% confidence intervals based on (a) fixed effects estimates, (b) random effects estimates from a mixed effects model, and (c) a Bayesian Markov chain Monte Carlo (MCMC) approach. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. We used the root means squared error for 95% confidence intervals for random effects estimates, and show the median and 2.5 and 97.5 percentiles for MCMC methods. Realized population change is the proportion of the initial population size remaining each year.

medium and long time scales, such as 5–20 years. Further, if a Bayesian approach is used to estimate Δ_t, uncertainty is portrayed more completely through the posterior distribution, and the probability of decline can be calculated. For the California spotted owl, values of Δ_t are more immediately interpretable than $\bar{\lambda}$ because interpreting differences in $\bar{\lambda}$ from 1.0 (stationary) depends on the time period, and summarizing how much a population will change over a given time period can be difficult. For example, estimated median $\Delta_{t\,\mathrm{MCMC}}$ was 0.78 for LAS, indicating that the population likely declined by 22% over the 18-year monitoring period. This is more directly interpretable than stating that estimated median λ_{MCMC} was 0.986 over the 18-year period. Although $\bar{\lambda}$ is an important metric of population performance, we conclude that Δ_t is generally more interpretable, particularly for depicting population changes over longer time periods.

Because estimates of $\bar{\lambda}$ and Δ_t can be biased by sampling variation, we recommend using a hierarchical Bayesian MCMC or a random effects approach to estimate these parameters. Both these approaches remove sampling variation and generally have improved precision as a result of reduced mean square error, and equal or improved coverage when compared to fixed effects estimators (Burnham et al. 1987, Link 1999, Burnham and White 2002). However, in this study, we found random effects estimates for Δ did not necessarily have improved precision. Although the average variance of the random effects point estimates of λ_t was less, 17–25% of the random effects estimates had variances that were 1.3–3.2× larger than their fixed effects counterparts. These large variances occurred when fixed effects estimates of λ_t were far from the random effects estimate; for example see SIE in 1992 and 1997 (Fig. 2). Because we added variances and covariances to estimates of Δ_t on the natural log scale, the few large variances propagated larger variances for subsequent estimates of $\tilde{\Delta}_t$ and, compared to their fixed effects counterparts, resulted in larger CIs for estimates of $\tilde{\Delta}_t$ for SIE and little reduction of the CIs for SKC.

We also found that the credible intervals on estimated median $\Delta_{t\,\mathrm{MCMC}}$ increased through the monitoring period, such that by the end of the 18 years they were similar to fixed effects CIs. This was not initially intuitive because the credible intervals for estimated median $\lambda_{t\,\mathrm{MCMC}}$ were smaller than the CIs of the fixed effects $\hat{\lambda}_t$. However, for these data we found relatively high proportions of negative covariances between fixed effects estimates that reduced the overall additive variance of subsequent estimates of Δ_t. Thus, the data and type of estimator (e.g., when the estimates of interest are the result of additive or multiplicative combinations) will determine whether random effects estimates or estimates from Bayesian MCMC methods

Table 3. Estimates of overall realized population change (Δ_t) for 3 estimators, which are based on estimates of annual rate of population change (λ_t). Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Overall realized population change is the proportion of the initial population size remaining at the end of the time period.

Study area	Estimator[a]	Δ_t[b]	SE	95% CI		CV (%)
LAS	FE	0.78	0.13	0.56	1.08	17
	RE	0.79	0.12	0.59	1.06	15
	MCMC[c]	0.78		0.57	1.08	
SIE	FE	0.85	0.15	0.60	1.21	18
	RE	0.84	0.18	0.55	1.28	22
	MCMC	0.89		0.65	1.20	
SKC	FE	1.27	0.24	0.88	1.83	19
	RE	1.16	0.23	0.79	1.72	20
	MCMC	1.22		0.82	1.84	

[a] FE are fixed effects estimates, RE are random effects estimates from a mixed effects model, and MCMC are estimates from 20,000 simulations.

[b] This estimate does not include the first 2 estimates and last estimate of λ_t because they were confounded or potentially biased.

[c] MCMC estimates are the median and 2.5 and 97.5 percentiles from the posterior distribution, based on 20,000 simulations.

will show improved precision compared to fixed effects estimates.

However, for estimating and removing process variation, a Bayesian hierarchical MCMC approach is generally preferable to the random effects estimator for a more practical reason. For the random effects estimator, a minimum of 9, and preferably 15, estimates are required (Efron and Morris 1977, Burnham and White 2002). Thus, the random effects method may be daunting in terms of required effort, or even impossible for many studies that lack sufficient spatial replication or temporal longevity. In addition, the variation in length of CI for random effects estimates (Fig. 2b compared to c) may not be readily interpretable and, therefore, may be less desirable.

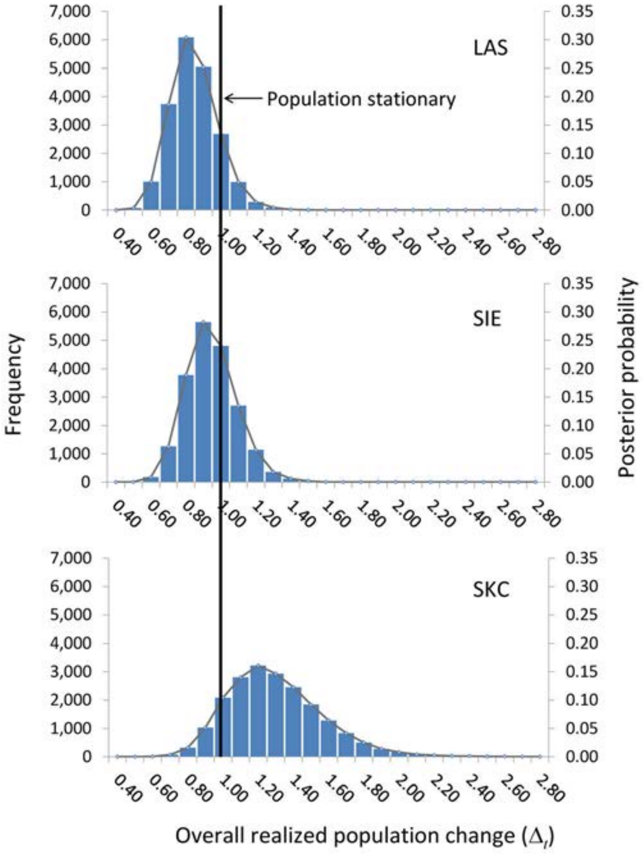

Figure 4. Estimated posterior distributions of overall realized population change (Δ_t) based on posterior distributions of λ_t from 20,000 Markov chain Monte Carlo (MCMC) simulations. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC])in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. Overall realized population change is the proportion of the initial population size remaining at the end of the monitoring time period.

Finally, we found that estimates of σ for mean λ were $\geq 2.9\times$ larger from the Bayesian MCMC approach compared to random effects estimates (Table 2). This is presumably because inference is exact and MCMC incorporates all uncertainty in the modeled system (Royle and Dorazio 2008, Higgins et al. 2009, Kéry 2010), thus providing a more realistic estimate of the variance of mean λ and Δ. In contrast, random effects estimates are based on maximum likelihood and are approximations with asymptotic properties, which means $\hat{\sigma}^2$ may be biased low for small sample sizes (Gelman and Hill 2007). In addition, unbiased estimates of σ^2 may be harder to achieve when σ^2 is small or sampling variation is relatively large (Burnham and White 2002). For the California spotted owl case study, the sampling variation was likely large relative to σ^2, resulting in estimates that were biased low or estimated as 0.

The biggest advantage of using a Bayesian approach and the posterior distribution of Δ_{MCMC} is that probability of decline can be estimated for a retrospective analysis, similar to how projection models or PVAs are used for a prospective analysis. In the past, evaluating whether the population declined typically relied on hypothesis tests with a null hypothesis of no decline. If the null hypothesis was not rejected, a retrospective power analysis was recommended to address the probability of accepting a false null or to determine the smallest detectable effect size, given study sample sizes (Taylor and Gerrodette 1993, Steidl et al. 1997, Lougheed et al. 1999). More recently, research has shown that retrospective power analyses are not appropriate to make inference about a non-significant result (Hoenig and Heisey 2001, Lenth 2001, Dixon and Pechmann 2005). Even if retrospective power was a valid approach, it still does not answer the real question of interest, what is the probability the population declined?

Table 4. Estimates of the probability of a population declining or increasing a given percentage or greater over a 17-year (SKC) or 18-year (LAS and SIE) monitoring period. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Probabilities are based on a posterior distribution of overall realized population change ($\Delta_{t\ \mathrm{MCMC}}$), which is the proportion of the initial population size remaining at the end of the monitoring time period.

	Overall decline in population							
Study area	**≥50%**	**≥30%**	**≥25%**	**≥20%**	**≥15%**	**≥10%**	**≥5%**	**>0%**
LAS	0.00	0.24	0.39	0.54	0.69	0.80	0.88	0.93
SIE	0.00	0.07	0.15	0.26	0.40	0.54	0.67	0.78
SKC	0.00	0.00	0.01	0.02	0.04	0.07	0.12	0.18

	Overall increase in population							
Study area	**≥0%**	**≥5%**	**≥10%**	**≥15%**	**≥20%**	**≥25%**	**≥30%**	**≥50%**
LAS	0.07	0.04	0.02	0.01	0.01	0.00	0.00	0.00
SIE	0.22	0.14	0.08	0.05	0.03	0.01	0.01	0.00
SKC	0.82	0.76	0.68	0.60	0.52	0.45	0.38	0.10

Hypothesis testing is a less informative evaluation compared to using a Bayesian approach to generate a posterior distribution of Δ_t. If the hypothesis is rejected, or if the 95% CI of estimated $\bar{\lambda}$ or Δ_t covers 1.0, even if barely, we have no way of evaluating the probability of a decline or lack thereof. The posterior distribution of Δ_t has broader application beyond use with Pradel model estimates of λ_t; it can be used for changes in density, abundance, or any population parameter of interest. For example, Gerrodette (2011) used data on the vaquita to examine the usefulness of frequentist versus other methods of hypothesis support for determining the change in abundance over an 11-year period. In a frequentist test for difference in abundance (i.e., overall change), $P = 0.38$, which did not mean abundance was equal, but rather that the data were not inconsistent with this hypothesis. However, although Gerrodette (2011) found a non-significant P-value when testing whether abundance had changed, Bayesian methods suggested a high probability of decline (0.88).

In our study, all CIs of estimates of $\bar{\lambda}$ and Δ_t covered 1. However, the probability of a decline varied widely between the 3 study sites, with LAS having a substantial probability of ≥10% decline (0.80), whereas SKC only had a 0.07 probability of the same decline. The problem of having a large probability of decline, even when the null hypothesis of no decline is not rejected, is especially important for small populations. Smaller populations can drop, undetected by a null hypothesis approach, to low levels where the probability of extinction increases to unacceptably high levels due to demographic variability and stochastic environmental events (White 2000, Lande 2001, Morris and Doak 2002). The undetected decline is a problem faced by ecologists studying sensitive populations. For example, even with 12–19 years of northern spotted owl (*Strix occidentalis caurina*) monitoring data collected on 13 study areas, Anthony et al. (2006) found that although 12 of 13 areas had estimates of $\bar{\lambda}$ that were <1, they could only conclude that populations were declining on 4 areas based on whether confidence intervals overlapped 1. Further, using Δ_t Anthony et al. (2006) were only able to detect a change in population for 6 of the 12 areas with estimated $\bar{\lambda} < 1$. Clearly, using a Bayesian approach to generate the posterior distribution of $\Delta_{t\ \mathrm{MCMC}}$ is a powerful tool for estimating probability of change and provides a more refined measure of risk to monitored populations, which is particularly significant when monitoring results affect the legal status of a species and have broad management ramifications.

Although measures of central tendency, such as mean or median λ and Δ_t, have the discussed advantages, they also have limitations. If a population is growing ($\bar{\lambda} > 1$), managers cannot tell whether the growth is from internal recruitment or immigration. Likewise, if a population is declining, managers cannot determine whether the declines are due to deaths within the population or emigration. Thus, additional information on specific vital rates is necessary to understand what is driving λ and ultimately, the mechanisms driving population dynamics. Although $\bar{\lambda}$ and Δ_t are important metrics, they may not suffice for a full assessment of a population's health. Ultimately, the choice of appropriate monitoring parameters should be based on management and conservation objectives and information needs, given available resources.

MANAGEMENT IMPLICATIONS

Managers and regulators charged with formulating conservation strategies for focal wildlife species require robust information to support decisions that are often ecologically complex and socially and politically controversial. Realized population change is a useful metric for assessing population trends of focal species. Further, using Bayesian MCMC methods to generate a posterior distribution of Δ_t is a valuable tool for robustly estimating risk, or probability of declines, for retrospective analyses of monitored populations. In addition, compared to a random effects estimator, Bayesian MCMC methods also provide a more broadly applicable approach for estimating mean or median λ and σ because they do not have the restriction of requiring ≥10 estimates. Finally, Bayesian MCMC methods are also preferable for point estimates of λ_t because they are exact for the data and, with sampling variation removed, their credible intervals are smaller than CIs for likelihood estimates. The Bayesian approach to generate a posterior distribution of Δ_t, in particular, provides biologists, managers, and regulators with more insightful information on the probability of population changes that can better inform conservation assessments and strategies.

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