

FINAL REPORT REVISION: CONTRACT #53-91S8-5-ECO54

**ACUTE EFFECTS OF CANOPY REDUCTION ON CALIFORNIA SPOTTED
OWLS:
CHALLENGES FOR ADAPTIVE MANAGEMENT**

22 August 2008

Principal Investigator: R. J. Gutiérrez
Department of Fisheries, Wildlife, and Conservation Biology
University of Minnesota
St. Paul, Minnesota

Assistant Project Leader: Sheila Whitmore
Department of Fisheries, Wildlife, and Conservation Biology
University of Minnesota
St. Paul, Minnesota

Cooperators:

Mark Seamans
Division of Migratory Bird Management
U.S. Fish and Wildlife Service
Laurel, MD

Guthrie Zimmerman
Division of Migratory Bird Management
U. S. Fish and Wildlife Service
Laurel, MD

Peter Stine
Pacific Southwest Research Station
U.S. Forest Service
Davis, CA

Perry Williams
Department of Fisheries, Wildlife, and Conservation Biology
University of Minnesota
St. Paul, Minnesota

THE EFFECT OF CANOPY REDUCTION ON CALIFORNIA SPOTTED OWLS: CHALLENGES FOR ADAPTIVE MANAGEMENT

Abstract:

INTRODUCTION

The effect of logging on spotted owls (*Strix occidentalis*) and their habitat has been one of the most pressing wildlife conservation questions facing western forest managers for the past 30 years. Two subspecies, the northern and Mexican spotted owls (*S. o. caurina* and *S. o. lucida*, respectively), have been listed as threatened, in part, based on the loss of habitat due to logging (Gutiérrez et al. 1995). Although not currently listed, the third subspecies, the California spotted owl (*S. o. occidentalis*), has been proposed for listing, again partly based on past losses of habitat and the potential for future habitat loss as a result of existing U. S. Forest Service (USFS) management guidelines (USFWS 2003, 2005, 2006). Despite these events and the concern over the effect of logging on the spotted owl, there has not been a single controlled experiment to evaluate these effects. This is noteworthy because the need for controlled experiments on spotted owl responses to logging has been recognized by biologists since 1984 (Gutiérrez 1985).

Executing a controlled experiment to examine the response of spotted owls to various approaches to forest management is problematic for two primary reasons, logistical challenges (e.g. timing of treatments, variability of logging crews, etc.) and the great variety of events that can occur under the rubric of “logging” on national forests. Logistical challenges arise because the scale of experiments must be very large to encompass natural variation in owl home range size, habitat composition and habitat selection behavior by owls, as well as ensuring that treatments are sufficiently large to enhance the possibility of a detecting a treatment effect should one occur. With respect to the second difficulty, the types of logging that could be evaluated require substantially different designs and considerations, not the least of which is the potential for a treatment to displace an owl pair from an established territory (in two of the spotted owl subspecies this would be considered a “taking” under the U. S. Endangered Species Act).

The impact of logistical challenges cannot be overstated because logging of public land requires a great deal of legal and professional preparation, including the bidding of contracts with specific constraints or conditions that are not usually encountered by logging contractors. Contract constraints or conditions may create uncertainty for logging contract bidders or even result in few or no bids, which could affect the sale of trees within territories. Consequently, researchers would lose direct control over the timing of logging treatments, and hence timing of treatments among treatment subjects (owls). Logistics also involve oversight and potential legal challenges by stakeholders who are concerned about the activity, which could affect timing of logging treatments differentially or eliminate them completely. Thus, it is not surprising that there have been no large designed experiments assessing the influence of logging on owls, despite the great interest in these affects.

In the case of the California spotted owl, the Sierra Framework (USFS 2004) proposed specific amounts, shapes, and distributions of forest (logging) treatments throughout much of the Sierra Nevada. The shapes and amounts of logging treatments had been hypothesized to reduce the rate of spread of wildfire based on simulation modeling (Finney 2001). These proposed forest treatments would consist of reducing canopy cover, tree density, and ladder fuels, but would not reduce the large trees commonly associated with spotted owl habitat in the Sierra Nevada (Gutiérrez et al. 1992). Thus, the primary objective of these treatments would be reducing the spread of large and severe wildfire with timber yield a secondary outcome that enables, through the revenues of sales, the treatment of a larger number of acres than would be possible with only appropriated funds.

The Sierra Framework was the culmination of extensive planning by the USFS to achieve a management strategy that could achieve multiple goals (e.g., reduce loss of forest and property from wildfire, protect wildlife and forest values, provide a modicum of economic benefit for local communities, and make the strategy financially feasible through limited timber harvest). The genesis of the Framework, from the perspective of the California spotted owl, was *The California Spotted Owl: A Technical Assessment of its Current Status* (Verner et al. 1992). The technical assessment (CASPO) was an interim plan that had many similarities to the Framework in terms of the design of logging treatments and retention of forest legacy elements and spotted owl habitat attributes (Verner et al. 1992). It was an interim plan until such time as specific uncertainties about spotted owls were understood or investigated and the USFS designed a new plan based on this new information. Intermittently, the Sierra Nevada Ecosystem Project (SNEP 1996) was undertaken, which was a Sierra-wide assessment that addressed multiple attributes of the Sierra Nevada ecosystem. The spotted owl was not an integral part of that project because the project's intent was to demonstrate the diversity and complexity of the Sierra Nevada ecosystem as well as the importance of its many attributes beyond the spotted owl. We believe this was an appropriate direction for SNEP because it, and CASPO, provided some direction to the Framework. Other plans were created and rejected by the USFS between the time of CASPO and the Sierra Framework (USFS 1993, 1996, 2001, FACA 1997). The past controversy surrounding any USFS management plan within the Sierra Nevada was expected given the diversity of stakeholders vested in the Sierra Nevada Ecosystem. Thus, the controversy over the management of the forests under USFS stewardship within the Sierra Nevada ecosystem has continued even with the implementation of the Sierra Framework.

Among the principle uncertainties noted in the Sierra Framework was the question of owl response to reduction in canopy cover. In response to this need, the USFS solicited research proposals to investigate responses of owls to canopy reduction following the implementation of Strategically Placed Land Allocation Treatments (SPLATS) within owl territories. Our study was designed to evaluate the effect of these SPLATS on spotted owls within their territories in the central Sierra Nevada. SPLATS are similar to the design of CASPO logging events except that the fuels treatments are laid out in a strategic pattern on the landscape (roughly a set of patches in a herringbone pattern perpendicular to the direction of the prevailing winds). This design has been demonstrated through computer simulations to have a significant effect on the rate of spread and intensity of a wildfire (Finney 2001). In April 2005, we proposed our study to

the USFS as a “pilot” adaptive management monitoring project (Walter and Holling 1990) to evaluate the response of California spotted owls to reduction in canopy cover in the central Sierra Nevada, California. Our study proposal was in response to USFS Solicitation number: R5-05-20-028; Title: B -- Spotted Owl Monitoring (hereafter RFP). This report will serve as a final report for that solicitation. Our report also will serve as an initial evaluation of a key uncertainty about the Sierra Nevada Forest Plan Amendment (SNFPA; USFS 2004: Vol. 1 pg 73), which was “*How do individuals and/or pairs of California spotted owls respond to reductions in canopy cover over some portion of their home range core area (HRCA)? Mechanical thinning of forests to reduce fuels hazards will address some ladder fuels and crown fuels in order to reduce the fuels condition class to acceptable conditions. This will reduce the number of trees by some amount (depending on pre-treatment stand conditions) with no trees greater than or equal to 30 inches diameter breast height (dbh) removed and will reduce crown closure by as much as 30% and down to as low as 40% average within a stand.*”

METHODS

Study Area

We studied the response of owls to canopy reduction in the central Sierra Nevada, California from 2005-2007. This region encompassed all or part of the Georgetown, Pacific, and Placerville Ranger Districts of the Eldorado National Forest; and on the American River Ranger District of the Tahoe National Forest (total area encompassed by these districts was 3188 km²). We estimated the area encompassed by the owls to be 2713 km² (1048 mi²). The general location of the study area was specified in the original RFP issued by the USFS for this project. The study area included all of the regional owl sites on the Eldorado spotted owl long-term demography study located on the Eldorado National Forest (Franklin et al. 2004). However, although some of the owl pairs used in the study did occur within this regional study area, no owl pairs were included from the existing, long-term density study area because of its confounding effect on trend estimates for owls in the central Sierra Nevada. The entire study occurred within the mixed conifer zone of these national forests because the vast majority of the spotted owls reside within this zone; we also eliminated owl sites in other habitats to preclude potential confounding effects related to differential response to canopy reduction by owls occupying different habitats (Gutiérrez et al. 1992, Verner et al. 1992). Owl habitat in these areas has been well described in previous studies (e.g., Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004, Chatfield 2005).

Experimental Design

Overarching philosophy of experimental design: The central purpose of our experimental design was to evaluate the response of owls to SPLATS in the central Sierra Nevada. SPLATS can be designed in a variety of ways to meet the primary objective of tempering the extent and severity of wildfire. These prescriptions also can be used simultaneously to influence other forest conditions such as regeneration of key species (e.g., *Pinus lambertiana*) or control of disease. Thus, the structure and amount of forest proposed for treatment can vary, largely as a function of the highly variable pretreatment conditions found on these forests, within an owl home range core area (HRCA), which precludes a

constant treatment effect. However, the general prescription for the amount of land treated for an effective SPLATs treatment should not exceed approximately 30% of the landscape or about 300 acres of a 1,000 acre HRCA. In our paper, we distinguish between “HRCA” and owl “territory” as follows: we use “HRCA” when considering the study design and owl responses with respect to a 1000 ac area surrounding the center of an owl’s activity area whereas we refer to “Territory” either as a reference location name for an owl or when we use it in a behavioral or general context. The essential purpose of a SPLAT treatment is to reduce tree density, canopy cover, and surface fuels such that the rate of wildfire spread is reduced when fire encounters a SPLAT (Finney 2001, USFS 2004). There may be other effects as well (e.g., reduction in understory vegetation). Therefore, we designed this study as a true experiment to examine the effects of canopy reduction on spotted owls while accounting for both the variability in the amount of area treated per owl HRCA and some key vegetation characteristics that were manipulated in SPLATs. However, we recognized that management issues could arise that could disrupt this design such that it would place our study in the realm of adaptive management experiments (Walters and Holling 1990). This recognition dictated the analytical methods we used. Nevertheless, we structured our design to minimize as many potentially confounding effects as possible (see below).

Potential owl response to canopy reduction treatments: Spotted owls could respond to logging (canopy reduction, tree reduction, and disturbance) in a variety of ways. Owls could respond immediately (acute response) and/or respond over a longer period (chronic response). Our study of owl responses occurred over a short period, one year; therefore, we assessed potential ways owls could respond in an acute manner. We hypothesized that the most likely acute responses would be their overt behavioral responses to treatments. For example, they could exhibit avoidance or attraction to treatment sites (indicated by shifting or displacement of owls from their original home range use areas). They could change the size of their home range to compensate for the potential loss of habitat or disturbance (they could also change the shape of the home range). They could change the distance they moved between foraging locations or how intensely they use treatments or other areas. They could incur stress from excessive treatment-induced noise or activity within their home range (Tempel and Gutiérrez 2003, 2004). Finally, they could die (mortality response) or emigrate (abandon) from their HRCA. The latter two responses would be severe, and emigration could be confounded with displacement (shifting of home ranges) because it would depend on the degree of shift that occurs, which is an arbitrary assessment.

It became apparent to us, given our restricted funds and the logistical challenges of monitoring birds over such larger and remote areas, that the only feasible response variables that we could estimate to evaluate acute response of owls to treatments were changes in sizes of owl home ranges and displacements of birds. Home range size can be estimated in ways that allow objective assessment of changes in home range size (see home range estimation below). Displacements can also be estimated using radio-telemetry locations (see below). We were unable to monitor changes in other behaviors such as movement rates, intensity of use, or other space use parameters because of the difficulty of getting even single locations for some birds would preclude meaningful analysis among birds. We were unable to use night vision goggles to observe owl behavior during harvest because of the excessive cost of goggles and the time it took to

locate birds for the telemetry. Some birds also were in extremely rough terrain, which precluded attempts to locate them at night far from roads. Finally, we were unable to secure ancillary funding to collect fecal samples to assay corticosterone levels as a measure of physiological stress in owls, so it was not feasible to devote time to collect fecal samples of birds.

Sampling population and selection of owls for sampling: Our potential sampling population included all spotted owls located in the central Sierra Nevada (Eldorado and Tahoe National Forests) that occurred on public land (the vast majority of owls in the area). We randomly sampled owls from this population, and randomly assigned them as treatments (birds receiving canopy reduction treatment) or controls (not receiving treatment) given specific constraints. We imposed constraints on selection of birds that would be “available for the experiment” from the central Sierra Nevada sample population *a priori* to the selection process. We felt these constraints were necessary to avoid confounding effects, and because some birds were unavailable for sampling (see criterion 6 below). These constraints were as follows:

1. Owls within the sampling population could not have had a major disturbance (stand replacing wildfire, SPLAT treatment, CASPO treatment, or other logging event) within their HRCA within the last 5 years.
2. Owls within the sampling population must have a minimum of 550 acres of suitable habitat within a 0.705 mile radius (1000 acre circular area) of a hypothetical HRCA such that treatments totaling a proposed 250 acres could occur while still retaining at least the owls’ Protected Activity Center (PAC) of 300 acres.
3. Owls that met criteria 1 and 2 must have the ≥ 250 acres “available” for treatment (i.e., it had to be accessible or logistically feasible to treat and also deemed “in need of fuels reduction”).
4. The majority of an owl’s hypothetical HRCA must be located on public land to avoid additional, unexpected logging impacts by private land owners.
5. Territories selected for sampling must have an owl pair. While this seems obvious, our initial pool of available birds was generated from a combination of the following: previous USFS owl surveys, the state of California spotted owl database, and our own extensive (23 years) spotted owl research in this region. Many of these historic locations had not been surveyed in many years. Therefore, it required us to survey all randomly selected territories to determine their occupancy status prior to their inclusion in the sampling pool. If we did not detect owls during subsequent surveys of a selected historic territory, we selected another territory randomly using the same criteria and then surveyed to determine owl occupancy. This process continued until the target sample population was achieved.
6. Birds unavailable for sampling were those who’s HRCA was located either entirely or mostly on private land. Owls that were part of the Eldorado density study area (Franklin et al. 2004, Seamans 2005) were not available for treatment because radio-marking could be a confounding effect for estimation of survival and reproduction of birds in this long-term study population (see Paton et al. 1991, Foster et al. 1992, Reynolds et al. 2004). Although not considered for this experimental study using radio telemetry, owls on the density study area were available for SPLAT treatment under Sierra Framework guidelines and will be used to evaluate the chronic effects (i.e., longer-term effects on occupancy, apparent survival and reproduction) of canopy reduction on owls of the

Eldorado study birds. Therefore, all birds on the Eldorado regional owl study population were made available for study, but we removed any birds that were selected for this canopy reduction study from future analyses of the long-term demographic trends for this study population.

Sample size: The RFP specified that 20-24 owls should be the sample size. We presumed that this number was based on our estimate of logistical capability given the funding level specified in the RFP. We believed that we could monitor 20-24 birds to gain reliable radio-telemetry data (see below) to estimate both home range size and shifts in home range areas given treatment. Therefore, we established a sample size of 24 birds (12 pairs occupying 6 treatment and 6 control territories) with the assumption that some of these birds would disappear (disperse or radios fail) or die as a result of natural mortality. We could not predict the sample size needed to detect a treatment effect because, as noted above, there was no prior information.

Types of treatments: According to our proposal, all treatments were designed to be consistent with the intent of the Sierra Framework (USFS 2004). The intent of the framework was to reduce the risk of large and severe wildfire by reducing tree density, understory vegetation, and reduction in canopy closure while leaving larger (>30 in dbh) trees. Thus, treatments could be single logging events occurring in one area or multiple logging events occurring in several areas. There could also be variation among treatments given the intent to treat specific stands with characteristics that “encourage” the spread or intensity of wildfire (e.g., stands with large overstory trees having a high density of small and medium sized trees with high canopy closure). Thus, variation in treatments was expected and the characteristics of the treatment were modeled as covariates accordingly (see below).

Temporal sequence of treatments and monitoring: We proposed that temporal sequence of the study would be as follows: 1) Spring 2005, identification of potential sampling pool and selection of sites based on criteria outlined above; 2) June 2005-January 2006, preparation and review of timber harvest plans and sale of harvest units; 3) Late Spring/Summer 2005, survey selected sites to determine owl occupancy and social status; 4) April-June 2006, capture and attach radio transmitters to owls found during 2005 surveys; 5) May-June 2006 radio-monitor according to sequence outlined in the “Field Methods” below to gather pre-treatment data; 6) July-August 2006, treat sites as prescribed to reduce canopy cover; 7) July 2006, monitor birds during harvest if possible; 8) August-October 2006, radio monitor birds to gather post-treatment data and begin removing transmitters; 9) April-May 2007 remove remaining transmitters from birds.

The actual sequence of timing became impossible to follow due to delays in implementing treatments. Most treatments were not completed before the end of September-October 2006. When we were alerted to the disruption of the proposed treatment schedule in July 2006 we developed an interim report that outlined not only the progress to date but also the potential consequences and alternatives for the study. The two alternatives were either 1) the study could be abandoned or 2) the study could be continued, but post treatment monitoring would be done in 2007. It was decided following a variety of meetings that the second alternative was most logical given our collective interest in pursuing these questions and that the majority of the budget had already been spent on the study as planned. It was discussed and recognized by the USFS and PSW that the delay would have unknown consequences for the original study

design because of the addition of a “year effect” and natural variation in movements of owls over time. At that time, it was also recognized and agreed that the study would be considered a pilot project that would guide future owl work and management with respect to harvest regimes or scientific study and monitoring. Thus, the temporal sequence of the study was changed to monitor post-treatment effects during 2007 because we did not have post-treatment information for some birds during 2006. This was the fundamental difference in the design. The obvious problem with the new design was that there could be confounding time effects (i.e., birds could move or behave differently over time that was independent of the experimental treatments). So it was agreed that we would pursue this redesigned monitoring of effects even though we recognized that we were potentially confounding the effect of treatments.

Field Methods

Location, capture, determination of social status, and marking of owls: We used standard techniques to locate, capture, determine social status, and band owls (Forsman 1983, Franklin et al. 1996). We assessed sex and age of detected birds by a combination of voice, plumage, and behavior (Forsman et al. 1983, Moen et al. 1991). We conducted a minimum of 5 surveys to determine occupancy of territories randomly selected for the study during 2005. When birds were detected, we assessed their social status and reproduction using standard protocols for the Sierra Nevada (Franklin et al. 2004, Seamans 2005), but we made no attempt to capture and band the birds during 2005 because of the potential to induce “trap shyness,” which would have impeded our ability to conduct the experiment.

Radio-telemetry: We used 11.4 grams (g) radio transmitters (Holohil Systems Ltd. model number: RI – 2C) attached to the owls with a backpack-style harness made from hollow Teflon-coated Kevlar tubing having a mass of 3-4 g. This transmitter and attachment configuration had a mass of 14.4-15.4 g and had been used with success on California spotted owls in the Sierra Nevada (Irwin et al. 2007, Dennis Rock personal communication). Expected life span for batteries powering these transmitters was 24 months). We used R - 1000 radio receivers (Communication Specialists, Orange, CA) and 3-element Yagi antennas to monitor radio signals emanating from the transmitters. Transmitter attachment on average took 29 min (range, 14 - 43 min). We were instructed and monitored by Dennis Rock on harness attachment during our first 3 captures.

We developed a two-tier random sampling scheme for monitoring radio-marked owls; one was based on order of bird and the other was based on time of monitoring. We randomly selected the initial order of sampling among birds. After initial selection, we realized that this would prove logistically unfeasible because birds monitored in a truly random fashion resulted in enormous wasted time moving between sites (e.g., it would take 6 hours to move between our most distant owl sites). Thus, we randomly selected a bird for a technician to monitor. We then selected the nearest birds to this original bird for monitoring by the observer. In one situation that required 2 hours one-way travel time to the site from our base site, we allowed that person to monitor that single bird the entire night because traveling to another site would have resulted in travel time of more than 3 hours (i.e., a total of 5 hours of driving, leaving little time to monitor >1 bird in a night). Once birds were randomly sampled they were monitored in sequence for a week. We then repeated the random sampling procedure. After a bird was randomly selected

for sampling we made sure all birds in that series were monitored throughout the night by stratifying sampling into three different time periods (sunset to midnight, midnight to sunrise, and occasional daytime walk-in locations). However, once a bird was located we continued to monitor that bird over a 3-hour period (note exception above where a single bird would be monitored for 4-6 hours due to travel time required to access this distant site) to ensure that birds were monitored at all times of the night to capture a representative sample of foraging/night time locations. If we did not locate a bird within two hours of initiating a sampling period, we abandoned searching for that bird that evening. We kept a table of monitoring times to determine if individual owls were not being monitored in all time segments of the night. When this occurred we made specific effort to sample that bird at times where samples were lacking.

Our study area and sampling design were not ideal for facilitating radio-telemetry (see discussion). Random selection of territories resulted in birds that had poor road access or in areas that were difficult to monitor (e.g., high proportion of rock and outcrops in territories which increased signal bounce; territories where roads were a long distance from owls, which made triangulation more difficult). However, key concerns in radio-telemetry studies have been precision and accuracy of signal bearings (Garton et al. 2001). Thus, we estimated bearing “error” by hanging transmitters in trees within representative owl territories, approximately 10 feet above the ground in locations that were unknown to the observers. We then required all observers to locate the transmitters following the same methods with equipment that they used while collecting data on the birds. Each observer collected 3 bearings on each of the 4 transmitters; they then repeated this procedure 3 times, so that each observer accrued 12 location estimates. We then calculated the difference between the true bearing and the observer’s bearing (error angle) for each bearing recorded. The standard deviation of all error angles was calculated for each observer (Ecological Software Solutions 1999). We averaged bearing error among all observers for each year to get the bearing error for that year (7.6° in 2006 [pre-treatment], and 9.2° in 2007 [post-treatment]). We established monitoring stations throughout all owl territories on available roads in a pattern that would facilitate triangulation (distance and angle between monitoring stations would be sufficient to triangulate on a bird’s radio signal). We estimated the location (UTM coordinates) of each station on our study area (and for the bearing error sampling) using a Trimble GPS unit. In the specific case of bearing error estimation we also used the GPS to mark the location of the radio transmitter being used in the test.

Following our bearing error estimation and training session each year, we used 3 criteria for locations we used in estimation of home range size and centroid location (see response variables below). Our criteria were that bearings must intersect to form a triangle; bearings must be ≥ 10 degrees apart, but not between 165-195 degrees apart; and all bearings must have been taken within 30 minutes of each other. However, we allowed no more than 5 bearings to derive a valid location. We used Program LOAS (Ecological Software Solutions, version 4.0.2.9) to estimate confidence ellipses for each set of location bearings and for estimating location bearing error ellipses during our bearing error trials. In addition, LOAS estimates confidence ellipses for each location and automatically adjusts location estimates using the assigned standard deviation of bearing error from our bearing error trials.

Habitat measurements:

Treatment sites

The number of vegetation plots ranged from 42-54 (except for Sugar Territory, which had 15, see results and discussion on this territory below). The number of treatment units within owl HRCA varied between 3-10, and the number of treatment acres ranged from 240-335 acres (except for Sugar Territory, which had 82 acres of treatment). The actual areas treated were probably slightly smaller than those given above because there were some watershed boundaries within the units that were not treated. For all territories (excluding Sugar Territory, for which there was no overlap with the HRCA) at least ½ of the treatment(s) fell into the HRCAs. Therefore, we sampled vegetation characteristics (see “*Vegetation parameters*” below) within treatment areas and control HRCAs that have been associated with spotted owls in the Sierra Nevada and elsewhere (Gutiérrez et al. 1992, 1995) to use as covariates when assessing owl responses to treatments. We established a grid of sampling plots with a density of one 0.2 ha (0.5 ac) plot for every 2 ha (5 ac) of treatment area across all treatment units to measure these characteristics (see below).

Control sites

The average number of harvest units in the treatment areas was 5.5 (not including the Sugar Territory). Therefore, we applied this number of “units” to all control HRCA to establish a sampling framework equivalent to the treatment areas for our vegetation plots and sampling intensity of control HRCAs. That is, in the case of control plots we selected similar sized “units” randomly within control HRCAs by randomly selecting polygons from a GIS vegetation layer that fell within the HRCA (some polygons may have extended beyond the boundaries of the HRCA, but we included them anyway because there were treatments outside of the HRCA boundaries of treatment owl HRCAs). We randomly selected vegetation polygons within which sampling would occur until the total area ≥ 250 acres.

We followed the strategy above for both Rob’s Peak Territory and ED028 because they showed relatively stable movements. In contrast, it was more complicated for the Dixie Queen Mine and Bald Mountain Territories because they exhibit large spatial shifts of territories. For these 2 sites we used the 95% fixed kernel estimates generated by the arcview extension, *Animal Movements* (Hooge and Eichenlaub, 1997), using the owl’s pre-treatment locations to define the vegetation polygons in which we sampled vegetation. We did this before we had estimated the final home range estimates. To determine vegetation sampling locations we placed a grid with a 125 m spacing of points over the 95% fixed kernel estimates. The Bald Mountain Territory kernel estimates were large, which would have resulted in a disproportionate number of plots relative to other territories so we randomly selected 55 locations using our sampling grid as vegetation sampling plots. However, we only sampled 49 plots because 6 plots were in barren areas such as log landing and yarding sites because the kernel areas included some private land that contained such areas, which provided no useful habitat information.

Vegetation parameters: We sampled a variety of vegetation characteristics in both treatment and control owl HRCAs. We sampled those characteristics that we believed might be informative to assess owl responses or those that we predicted would change as

a result of treatment. High canopy cover has been associated with California spotted owls (Gutiérrez et al. 1992) so it was reasonable to assume that reductions in canopy could have a negative effect on owls. Thus, we sampled canopy cover using a sighting tube (densitometer) and canopy closure using a concave spherical densiometer (Jennings et al. 1999). We used only the canopy cover estimates in our analysis. However, the Sugar Territory was retrospectively switched from a control to a treatment so we used estimates of canopy cover derived during our pre-treatment sampling of randomly selected vegetation plots (see Discussion below). At each plot, we took 50 measurements with a sighting tube along two 25 m measuring tape-line transects established through the center of the plot. We calculated mean values from these 50 measurements to give a representative measure of percent canopy cover at that plot. We took 16 measurements of canopy closure using the spherical densiometer: 1 from each cardinal direction from 4 locations that were along the transects, 4.5 m from the center of the plot. We counted all trees ≥ 15 cm (6 in) within a fixed-sized plot of 0.05 ha (0.12 ac), and trees ≥ 76 cm (30 in) within a 0.2 ha (0.5 ac) plot. Spotted owls characteristically inhabit forests that have a “J-shaped” diameter distribution and contain large trees (Gutiérrez et al. 1992, Moen and Gutiérrez 1997). Therefore, we estimated tree sizes by measuring the diameter of individual trees at breast height (dbh) within those plots using Biltmore sticks and diameter tapes. Spotted owl habitat often has coarse woody debris as a component (Gutiérrez et al. 1992) so we counted logs with a large end >25 cm (10 in) that fell within the 0.05 ha (0.12 ac) plot. We also estimated slope with a clinometer, aspect with a compass and cross checked with a topographic map, and elevation with an altimeter.

Analysis of Data

Home range estimation: To estimate home range size during pre- and post-treatment periods, we only used locations for which a confidence ellipse ≤ 7.5 ha was estimated by LOAS. We used program *Animal Space Use* (ver.1.0; Horne and Garton 2006a) to compare home range estimators using an information theoretic approach to evaluate the home range estimator that was the best fit for our data (Horne and Garton 2006b). We compared the following home range estimators: adaptive kernel, fixed kernel, 2 mode bivariate normal mix, 2 mode bivariate circle mix, 1 mode bivariate normal, and exponential power model. We used a likelihood cross-validation criterion (CVC) to select the top model. Likelihood cross-validation (Cvh) was also estimated in *Animal Space Use*, which we used as the smoothing parameter in estimating pre- and post-treatment kernels (program BIOTAS, version 2.0, Ecological Software Solutions, 2004) as suggested by Horne and Garton (2006c). We exported 50%, 75%, and 95% kernels into the GIS.

Estimation of displacement: We estimated the centroid of the radio locations that fell within the 95% adaptive kernel for each bird for both the pre- and post-treatment periods. The centroid of all spatial locations was not of interest per se, but we used the distance between pre- and post-treatment periods as a measure of “displacement” (home range shift) of the home range because one potential response of owls to treatments (potential disturbance response) could be to shift their home range as measured by the collection of telemetry locations from its original location to a new location. This would not necessarily be an abandonment of a home range but could be a response to use other

areas within a home range that happened to be further from the treatment. We estimated two types of response: simple displacement and displacement relative to the treatment. In the first case, we estimated the gross difference between centroids of treatments vs. controls birds. In the second case we estimated the difference between the centroids of treatments vs. controls relative to a reference point. For treatment birds, this reference point was the boundary of the nearest treatment to its centroid. For control birds, this reference point was a random point that was selected between the outer boundary of a 121 ha (300 ac) imaginary circle and an imaginary boundary described by a circle of 2794 ha (6903 ac). This “donut” area was based on the distance that the furthest treatment unit occurred from a treatment bird. Our 121 ha (300 acres) simulated the area of a PAC, which by design of the experiment was supposed to be a protected area for the owls. In practice, it was difficult to know where the owls were prior to the layout of treatments because we had no knowledge of home range use of the owls before the timber sales were issued for bid. Consequently, we felt that an arbitrary area of a 121 ha (300 ac) “PAC” around the control centroid served the same purpose of a simulated “protected” area. We predicted that owls in control territories would move randomly with respect to these random reference points, whereas, if owls avoided treatment areas there would be a movement away from the treatment.

Estimation of Habitat covariates: We estimated individual habitat covariates from sampled vegetation data. We considered snags (standing dead trees) separately from live trees in our habitat evaluations. We estimated snag and live tree basal area (BA) from our tree diameter measurements, and density for small snags, large snags, small trees, and large trees from our plot count data using standard equations (Table 1).

We estimated the proportion of suitable owl habitat (i.e., amount of “selected” habitat in CASPO, Verner et al. 1992) within an owl’s home range in the following way: First, we estimated the 95% adaptive kernel for each owl pre- and post-treatment. Second, we overlaid this 95% adaptive kernel onto a spatially explicit vegetation map of the site for which we had done extensive ground sampling and verification over many years (see Chatfield 2005, Seamans 2005). Third, we estimated the area of each vegetation polygon with the 95% adaptive kernel home range of each owl. Fourth, we selected all polygons whose vegetation was classified as size class 5, 6, or 7 (medium forest high canopy; large forest low canopy; large forest high canopy, respectfully; see Chatfield [2005] for a description of these general descriptions). Finally, we summed the areas of classes 5, 6, and 7, and divided by the total area of all polygons in the kernel to derive the proportion of “suitable” habitat within the owl’s 95% adaptive kernel home range area.

Model Selection: We used generalized linear models and model selection approach to assess whether treatments (predictor variable) influenced spotted owl behavior (response variable [see “response variables” above]). We developed three sets of models based on the response variables: (1) change in home range size, (2) general pre- and post-treatment home range displacement, and (3) displacement of home ranges relative to treatment locations. For changes in home range size we predicted that the treatments, which resulted in reductions in amount of suitable habitat or disturbance, would result in owl’s expanding their home ranges to compensate for the loss of habitat. We estimated home range size for each control and treatment owl prior to treatments and after treatments (see

above). We calculated the change in home range size by subtracting pre-treatment home range size from post-home range size (i.e., positive values indicate that the home range increased in size whereas negative values indicated that home ranges decreased in size). For displacement of home ranges, we considered two response variables. First, we hypothesized that owls would shift their home range core areas to avoid the treatment area, avoid treatment disturbance, or compensate for the loss of habitat. They could do this by moving in any direction, even toward and then beyond the treatment to sequester additional habitat. Thus, displacement would not necessarily be relative to direction of the treatment from the original home range centroid. We calculated this home range displacement by calculating the increase or decrease in centroid distance between the pre-treatment home range centroid (i.e., geometric center of all valid radio telemetry locations taken during the pre- or post-treatment periods that fell within the 95% adaptive kernel; the geometric center is the mean of all x-coordinates and the mean of all y-coordinates of telemetry locations within an owl's home range) and the post-treatment home range centroid. Second, we hypothesized that the owls subjected to treatments would move away from the treatment (a directional effect). We then estimated home range displacements or movements relative to the treatments by estimating: (1) the distance between the treatment stand (i.e., reference point) and the pre-treatment home range centroid, (2) the distance between the post-treatment home range centroid and the same treatment stand in the first step, and then (3) calculating the difference between the two distances. To estimate displacement of controls, we used a randomly selected point between 622 m and 2982 m radii from the geometric center of control territories as the reference point (for selection of reference points see *Estimation of Displacement* above).

Due to the small sample size, we were concerned that confounding factors such as the amount of habitat within an owl's HRCA (i.e., inherent variation in territory quality) might reduce our ability to detect treatment effects. Therefore, we included habitat predictor variables as covariates in addition to the treatment effect. We used model selection to compare models representing a combination of the following habitat variables: percent of spotted owl habitat in pre-treatment home ranges, percent canopy cover in home ranges prior to treatments, and density of large diameter trees in pre-treatment home-ranges. We estimated pre-treatment habitat conditions at the sites to be treated for the treatment territories, whereas we used the sampling strategy based on sites within a hypothesized home range core area for controls (see above). We chose the three habitat characteristics described above (pre-treatment habitat, pre-treatment canopy, and density of large trees) after examining all habitat information collected during vegetation sampling. We rejected habitat characteristics for which data were missing (i.e., the characteristic did not occur within some territories, was correlated with other variables, was less informative to managers [SPLAT design]), and retained those that were essential features of the study (i.e., amount of owl habitat, canopy cover and large trees). These three habitat conditions have also been key attributes in owl management within the Sierra Nevada. We predicted that owls exposed to treatments would increase their home ranges and move more than those not exposed to treatments. However, we assumed that this potential treatment effect may be modified by baseline habitat conditions within territories. We predicted that spotted owls in territories with less pre-treatment spotted owl habitat, lower percent canopy cover, or lower tree density would increase their home range and move more than those having higher amounts because it appears that birds

having more habitat in their home ranges are more fit than those birds with less habitat (Seamans and Gutiérrez In Prep). We quantified the treatment effect two ways. First, we considered the treatment effect as an categorical predictor variable where treatment birds were assigned a 1 and control birds a 0 in all models. Second, we considered the treatment effect as a continuous variable where treatment territories were assigned the area harvested (in acres) and control birds were assigned 0. We developed seven models representing various combinations of these predictor variables (Table 2). We conducted three sets of model selection exercises by comparing each of the seven models for each of the three response variables.

We used Markov Chain Monte Carlo techniques to estimate model parameters (Gelman and Hill 2007) in program WinBUGS (Spiegelhalter et al. 2003). We assumed that the measured response variables were samples from a normal distribution with unknown precision and a mean that was a linear function of the predictor variables:

$$Y_i \sim N(\beta_o + \beta_j * X_i, \omega),$$

Where Y_i represented the response variable for the i^{th} bird, the β_o represented the intercept of a linear function, β_j represented the unknown parameters relating the effect of the j th predictor variable to the response variable, and ω represented the unknown precision. We used non-informative normal priors [N(0.0, 1.0 * 10⁻⁶)] on all β parameters and non-informative inverse gamma priors [GAMMA(0.001, 0.001)] for the precision. We ran 3 chains of 80,000 iterations (estimates) each and used a thinning factor of 10 (i.e., for each chain, 8,000 estimates from the 80,000 iterations (estimates) were retained for making inferences). Further, we used the first half of the iterations for the burn-in period to allow model convergence and presented parameter estimates based on the last half. Thus, we presented parameter medians and 90% credible intervals based on the 4,000 final iterations (estimates) retained from thinning. We inspected history plots of the three chains and density plots to ensure that models converged. We used deviance information criteria (DIC) to compare the relative fit of each of the seven models for each response variable (Congdon 2003). We considered models with the lowest DIC value as the most parsimonious. In addition, we used the median value from the posterior distribution to make inferences.

RESULTS

We randomly selected 12 territories from the central Sierra Nevada (Tahoe and Eldorado National Forests), which were distributed across an area of 271,320 ha (670,446 acres). Appendix 1 provides a history of each territory selected for potential study. The farthest straight line distance between owl territories was 68.6 km (42.6 miles) based on the distances between the furthest centroids of 95% adaptive kernel home range estimates. During 2005, we located 11 pairs and 1 single owl at the 12 territories originally selected randomly from the population of owls thought to have met *a priori* criteria for selection (see above and Table 3). However, we had to drop 2 territories from our original group of 12 because they failed to meet the original selection criteria even though we were assured that the owls we randomly selected had met the criteria (i.e., it was determined by the USFS in late August 2005 that they could not be logged for logistical reasons). We then randomly selected 2 more potential territories to replace these discontinued

territories, but this very late determination of logistical limitation resulted in insufficient surveys for territories we randomly selected as “replacement” territories – see Table 3 and Appendix 1). Despite this time limitation, we located 3 birds in these replacement territories during September 2005 (Appendix 1).

Thus, we surveyed 14 territories in 2005 and detected 27 owls (13 pairs, 1 single). After dropping 2 of the original territories, we began 2006 with a potential sample population of 12 territories (23 birds distributed as 11 pairs, 1 single). We did not detect 8 birds at these territories despite repeated, intensive surveys (Table 3, Appendix 1). However, we detected a female in ED200 Territory that we did not detect in 2005. Thus, we detected 16 birds in 2006. The large number of surveys completed in 2006 suggested that the birds were absent (i.e., standard criteria for being unoccupied or missing requires several surveys to a particular territory; Franklin et al. 2004, Blakesley et al. 2006). Coincidentally, this low rate of “apparent” survival was consistent with banded owls on the Eldorado study for this same time period; the winter of 2005-2006 revealed the lowest apparent survival for the Eldorado study population since the study’s inception (Seamans and Gutiérrez 2007, Gutiérrez and Tempel 2008). The fate of these missing birds was unknown. Usually it will difficult, if not impossible, to determine if a bird was missing due to mortality, emigration, or simply not responding to conventional methods of detection. We were unable to capture 2 birds in 2006 despite repeated attempts. Therefore, we successfully captured and radio marked 14 birds (see Appendix 1 for a complete history of each bird), which was well below the target sample size of 24 birds. The original target sample size was set by funding level and the assumption that some (approximately 4 birds specified in the proposal) birds would be lost due to natural mortality, dispersal, radio failure, or failure to capture the owls. However, natural mortality/dispersal alone was twice our expected *a priori* “loss” rate. Of the 14 birds captured and radio marked we lost 1 bird (female at Bald Mountain Territory) 3 months after capture when it was apparently hit by a vehicle on Wentworth Springs Road (see Appendix 1). We radio marked 1 bird (the female at Sugar Territory) that disappeared soon after marking, only to be found dead in 2007 (Appendix 1). In 2006, we detected a weak signal from this bird’s transmitter coming from a very deep, rugged canyon that we could neither accurately triangulate nor find during walk-in surveys to locate the bird. This bird’s transmitter was still working when we recovered her remains in 2007. We monitored 1 bird (female at Dolly Territory) throughout the pre-treatment period, but not during the post-treatment because it either dispersed, died, or its radio failed (i.e., we were uncertain about its fate [Table 3, Appendix 1]). We monitored 1 bird (a male at ED124 Territory) for a sufficient period of pre-treatment time, but it subsequently disappeared and its fate was unknown. Finally, we suspected that 1 female caught at ED200 territory was a “floater” because she exhibited large, erratic movements during both the pre- and post-treatment periods so we excluded her from analysis. These various losses resulted in a final study population for which we derived usable data of 9 owls (5 control and 4 treatment owls). All owls alive at the end of the study were recaptured and their transmitters removed even though this extended our recapture period well into 2008 (Table 4, Appendix 1).

Home range estimation: Below we only presented results for owls that we included in the experimental analysis. We had sufficient data to estimate the 2006 home ranges of additional owls, which will be presented elsewhere (Williams, M.S. Thesis, University of

Minnesota in progress). Of the 9 owls that we monitored over periods ranging from 399 to 443 days, we obtained between 54 and 105 useable (i.e., valid by bearing error criteria) pre-treatment locations and between 60 and 138 post-treatment usable locations for these birds (Table 4). Thus, we believed we had sufficient data to estimate home range size and displacement of birds between the pre- and post-treatment periods. The adaptive kernel estimator was selected more times than other estimators for each owl's pre-treatment home range estimation (6 out of 9) home ranges were best estimated by the adaptive kernel density estimator; Table 5). We only used pre-treatment home range estimates because we were interested only in selecting a parsimonious estimator relative to our data and not how treatments or time might affect the selection of an estimator. Further, the kernel estimators are non-parametric so AIC_c cannot be used to order the selection of these estimators (Horne and Garton 2006 b,c). Therefore, we used this estimator in all subsequent analyses. We also have created individual maps of these 95% adaptive kernel density home range estimates with individual radio locations plotted to aid management of these birds.

Changes in owl habitat as a result of treatment: We qualitatively summarized the results of the treatments on the key vegetation characteristics of interest that we used in our modeling to assess whether habitat change occurred as expected rather assessing the degree of statistical change. Canopy cover decreased in all treatments if one assumes the treated site at the Sugar Territory had canopy cover estimates similar to the locations within where we estimated pre-treatment canopy cover (Table 6). Similarly, the proportion of suitable habitat changed for all birds from the pre- to post-treatment periods. All 5 control sites showed an increase in the proportion of suitable habitat in their home ranges between time periods, but 3 of these differences were small (<9% [BALDM male, ED028 male, ED028 female]). In contrast 2 of 4 treatment birds showed a decrease (although 1 of these differences was small [<3%], SUGAR male, Table 6) between time periods.

Effects of canopy reduction on home range size: Although we estimated a larger home range size for both control and treatment owls during the second year of study, control owls appeared to increase their home ranges more than treatment owls ($\bar{x}_{\text{control}} = 191.28$ ac, SD = 157.11 ac, and $\bar{x}_{\text{treatment}} = 113.35$ ac, SD = 482.98 ac; Table 7). A model representing the additive effects of pretreatment canopy closure and total area treated was ranked highest (Table 8). However, an intercept only model (i.e., a null, means model, or no treatment effect) closely competed (≤ 2 Delta DIC) with the best model. Model parameters from the best model indicated that the amount of canopy closure pre-treatment had the strongest correlation with changes in home range size (median $\beta_{\text{pretreatment canopy closure}} = 13.88$, 90% CI = 0.39 to 25.54), suggesting that territories having higher amounts of canopy closure prior to treatments tended to increase in size between the first and second year more than territories having less canopy closure. The 90% credible interval overlapped zero for area treated (median $\beta_{\text{area treated}} = -0.18$, 90% CI = -1.58 to 1.10) indicating a weak or no correlation between this variable and changes in home range size.

Effects of canopy reduction on displacement of home range: The home range center as defined by the geometric mean (i.e., centroid) of all telemetry locations falling within the boundaries of the 95% adaptive kernel of treatment owls appeared to show greater displacement between years than control owls following canopy reduction treatments

($\bar{x}_{\text{control}} = 12984.40$ ft, $SD = 14624.65$ ft, and $\bar{x}_{\text{treatment}} = 13591.00$ ft, $SD = 19159.13$ ft; Table 7). A model including a categorical treatment effect and the proportion of an owl's 95% adaptive kernel home range comprised of spotted owl habitat during the pre-treatment period was 1.95 DIC units better than the second-ranked model (Table 8). The 90% credible interval for the treatment effect parameter overlapped 0, indicating no statistically significant effect of the treatment on displacement of the centroid (median $\beta_{\text{treatment effect}} = 38.27$ ft, 90% CI = -1583.00 to 1716.00). This model indicated that home ranges of owls having a higher proportion of suitable habitat during the pre-treatment period tended to have greater displacement than owls having a lower proportion of suitable habitat in their home range (median $\beta_{\text{pretreatment habitat}} = 331.9$ ft, 90% CI = 95.61, 558.30). Although this best model showed a strong influence of pre-treatment habitat on owl movements, it explained only 39% of the overall variance ($\sigma_{\text{best model}}^2 = 2.53 \times 10^8$; $\sigma_{\text{means model}}^2 = 4.18 \times 10^8$). The second-ranked model also indicated a strong correlation between the displacement variable and pretreatment habitat (median $\beta_{\text{pretreatment habitat}} = 284.00$ ft, 90% CI = 6.96, 562.90), but no other correlations.

Effects of canopy reduction on displacement of home range relative to treatment locations: In this analysis we hypothesized that owls, if they were negatively impacted by logging in the short-term, would move away from treated areas. The centroids of owl territories undergoing treatment tended to be displaced further from the treatments than control birds were displaced from random points selected from within a similar sized area within which treatments were undertaken in the treatment owl territories ($\bar{x}_{\text{control}} = 10550.80$ ft, $SD = 14625.42$ ft, and $\bar{x}_{\text{treatment}} = 12007.75$ ft, $SD = 19677.99$ ft; Table 7). Model selection results for this response variable were very similar to the previous response variable (Table 8). The best model, which represented a categorical treatment effect and proportion of pre-treatment suitable habitat in the home range, was ranked 1.98 DIC units better than the second-ranked model. Similar to the general displacement response variable above, the 90% credible interval for the treatment effect indicated that we could not detect a statistical significant effect of the treatment given our sample size and variation (median $\beta_{\text{treatment effect}} = 34.67$ ft, 90% CI = -1587.00, 1714.00). This model indicated that owls having a higher proportion of suitable habitat in their home ranges before treatment tended to have larger displacements relative to treatment patches (in the case of treatment owls) or random points (in the case of control birds) than birds having a lower proportion of suitable habitat in their home ranges (median $\beta_{\text{pretreatment habitat}} = 249.8$ ft, 90% CI = 60.51, 520.10). This model explained only 33% of the total variation ($\sigma_{\text{best model}}^2 = 2.50 \times 10^8$; $\sigma_{\text{means model}}^2 = 3.74 \times 10^8$). The second-ranked model did not have any variables with a strong correlation to the response.

DISCUSSION

The habitat associations of the California spotted owl has been of long-standing interest to biologists and forest managers in the central Sierra Nevada (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). Moreover, the observed relationships between owls and older forest has placed

conservation focus on the effect of logging on spotted owls, and has been a long standing and controversial issue (Gutiérrez 1985, Simberloff 1987, Gutiérrez et al. 1995). It has been assumed because of the owl's observed habitat relationships that logging negatively affects spotted owls because of trends in spotted owl numbers and distribution appeared correlated with loss of habitat through logging (Forsman et al. 1984, USFWS 1992 a, 1992 b, USFWS 2003, 2005, 2006, Anthony et al. 2006). Unfortunately, correlative studies cannot invoke causation so it has also long been argued that experiments are needed to provide reliable knowledge about the effects of logging on spotted owls (Gutiérrez 1985, Noon and Franklin 2002). Our study represents the first true experiment designed to examine the effect of canopy reduction via logging on the spotted owl. We designed our study to provide direct causal links between logging and acute (short-term) effects on spotted owls. The results of our study were equivocal; however, we feel they provide a basis for designing and monitoring effects of logging on spotted owls. For example, a much larger sample population should have been selected for study because of natural attrition and demonic/non demonic intrusions (Hurlbert 1984) that reduced our sample size far beyond our expectations. In retrospect, we felt that more control should have been exerted over the timing and execution of treatments to reduce time-confounding effects. Finally, sufficient funds should have been allocated to achieve the previous two suggestions (see also "Management Implications" below).

Effect of logging on forest structure: As noted above, we were only interested in a qualitative change in forest structure related to canopy reduction. In all cases (assuming the pre-treatment canopy cover estimates at random sites within the Sugar Territory reflected the conditions of the site actually logged, see below for discussion of design execution), the percent canopy cover was reduced at the treatment sites. Similarly, the density of large trees (>30 dbh) decreased between the pre-treatment and post-treatment sampling at 3 of 4 treatment sites. However, these declines were relatively minor. We hypothesized the differences between the pre- and post-treatment measurements in large tree density could be related to four sources of variation: sampling error, logging mistakes, logging engineering, and "hazard" tree removal. Sampling error could have occurred because the exact same center points for sampling plots were not always consistent between the pre- and post-sampling periods. We marked the pre-sampling plots with both flagging and aluminum tags attached with aluminum nails to reference trees as well as recording a GPS location at plot center. However, some of these references marks were destroyed during logging, as expected, and there was some inherent variation in GPS readings between recordings. Thus, if the center of the sampling plot was not exactly the same then it is possible that there was variation in plot location. In addition, large trees were counted as "in" or "out" of the plot by using a range finder, for which there is some minor error when using this device. Some large trees were probably harvested by mistake, especially those close to the diameter retention limit. This probably resulted in some slight variation in tree density estimates. We noted that some large diameter trees were taken where log landing sites were constructed or where there were skid trails. Finally, some large trees along roads were harvested and these could have been deemed "hazard" trees, which are often harvested during logging operations. All 4 of these sources of potential variation probably contributed incrementally to the decline in large tree density we observed. However, it was our

opinion that generally the estimates of forest characteristics showed that the logging produced the desired effects of reducing canopy closure, retaining larger trees, and reducing ladder fuels and understory (these latter characteristics were not measured but our visual inspections of post-treatment sites made this conclusion inescapable). Interestingly, we expected to observe a greater decrease in canopy cover than we did because the guidelines for SPLATS are quite broad (decreases to 40% are possible). The range of canopy reduction we measured using densitometers was approximately 10-13%. This is a relatively small change given the wide latitude that is allowed under the treatment guidelines. This small decrease could be eliminated by normal tree growth in a few years. Post-treatment increases in proportion of suitable habitat within all 5 control territories were attributable to range displacements (shifts) between periods because we were sampling new HRCA that had different relative proportions of habitat within them. However, it was not clear if the decrease in portion of suitable habitat in treatment territories was due to treatment effects and/or shifts in home range by owls in response to treatments, where such shifts resulted in lower amounts of habitat within the new HRCA (see also below).

Effects of canopy reduction on home range size: The top model in this analysis (additive effects of pre-treatment canopy closure and area treated) suggested that territories having a higher percent canopy closure during the first year tended to increase in size from year one to two more than territories having lower canopy closure. This result was counter to our *a priori* predictions because higher canopy closure should be indicative of better habitat and owls inhabiting better habitat, theoretically, should have both smaller and more stable home range sizes. However, our second-ranked model (null model) was closely competing suggesting uncertainty about the results of this analysis. In considering this unexpected result, it is possible for spotted owls, with their very large home ranges (larger than predicted based on their body size), are a reflection of either patchy distribution of prey or variability in prey density across their home range (Carey et al. 1992, Ward et al. 1998). Thus, birds with better habitat (either more area or higher quality) might have more options to expand their home range over time. The alternative could also be true that habitat with higher canopy closure might have lower prey densities so that birds having home ranges characterized by high canopy closure might be more likely to expand or change home range size. There were several other possibilities we considered when trying to reconcile these results. First, the models could be poorly conceived. Second, the sample size may have been too small relative to the variation in the data to detect an owl response. Third, the delays in executed treatments and other implementation issues related to the design execution could have introduced several confounding factors that added additional variation that obscured the results as we suggested in our explanation of the implications for changing the design (see “Experimental Design” above). Given these possibilities, we believe that our models are sound, at least conceptually, because they reflect both quantitative and qualitative treatment effects of habitat and home range conditions (pre-existing habitat, canopy cover, and tree densities) hypothesized to be relevant to California spotted owls. We also believe that our sample size was too small given the substantial variation within and among treatment and control birds, which introduced a real possibility of chance results in our analysis. We are currently working on this issue of sample size estimation for a study of this type

given our data. Finally, we believe that the implementation problems led to substantial confounding of results (e.g., delay in timing of treatments, unequal pre- and post-sampling times, natural changes in owl behavior compounded with potential responses to treatments, and inadvertent logging of a control). Despite our uncertainty we believe the effect of canopy reduction on spotted owls can be tested in the future with a design like ours but contingent on a more rigorous execution of the sampling design (see “*Specific recommendations for adaptive management*” below). The loss of birds to natural causes was unexpected and lowered our sample size to a level that made interpretation of results more difficult. It is unlikely that a study population such as ours would experience such a high natural mortality during an experiment, but it must be considered when planning future experiments. Thus, we cannot draw firm inference from these results although we believe that our models are sound and our results could be used as prior information for future study design and Bayesian modeling.

Effects of canopy reduction on general displacement of home range: Treatment owls appeared to show greater general home range displacement than control owls but this was related more to the amount of pre-treatment habitat than it was to the treatment effect itself. The second ranked model was competing and was similar except that the treatment effect was continuous and not categorical as in the top model. A means model was not a competing model. Although our top model explained more variation (39%) than we expected given the change in study design, we do not feel confident in the variance components analysis because the small sample is insufficient to derive an accurate assessment of the variance explained by these models. The top model also suggested that birds with more habitat before treatment tended to move more than those with less habitat. This suggests that most owls were shifting their home range cores to varying degrees between years. We know from other research on spotted owls that annual variation in weather and related ecological factors (e.g. cone crop, small mammal abundance) can overwhelm any influence of habitat for certain response variables such as reproduction, which might be what we are observing here. The model result was somewhat counterintuitive in that one might expect that birds with more habitat would be less likely to move, but when considering owl responses in general and spatial distribution of owls with respect to habitat this result seems plausible. We term this idea the “more options hypothesis,” which posits that owls having more habitat within their home range or within their general landscape area, perhaps coupled with a landscape unsaturated by owls, can shift home ranges more easily to compensate for habitat disturbance or changes in other factors such as prey density within patches (see Cary et al., 1992). Such a hypothesis would also be consistent with Seamans and Gutiérrez (2007, Unpublished data) who showed that birds having more habitat are more likely to have higher occupancy and contribute more to the dynamics of local populations than those birds having less habitat in their territories. That is, birds with better habitat on a larger scale have more options to compensate for harsh years, allowing them to continue to reproduce by shifting their home range and increasing their home range size. In contrast, individuals with poor habitat simply forgo reproduction and wait for better conditions because their only other option is to disperse to a new territory. Nevertheless, the fact that owls may be able to move or adjust home range size following disturbance is only an acute response whereas disturbances may result in a deterioration of the owl

territories such that these birds suffer a loss of fitness (chronic effect) because of habitat loss (see also Seamans and Gutiérrez et al. 2007 for a simulation of the effect of habitat loss on spotted owls).

We believed these results could have stemmed from all the conjectures and hypotheses stated above. In particular, we believe that a pattern may be emerging that is consistent with earlier occupancy analysis (Seamans and Gutiérrez 2007) and simulation modeling of potential habitat loss on population dynamics (Seamans and Gutiérrez, Unpublished data) that indicates spotted owls having high amounts of habitat in their territories have higher occupancy rates and contribute more, proportionally, to population rate of change than owls having low amounts of habitat their territories. Thus, if an owl occupies a territory with much habitat and it is disturbed it can actually move whereas a bird occupying a territory with limited habitat may be constrained in its response to disturbance. As noted above, this ability to move may only have short-term benefits, which would not mitigate the deterioration of its territory over a longer period of time.

Effects of canopy reduction on displacement of home range relative to treatments:

Spotted owls whose home ranges were treated tended to move further from treatments than control birds tended to move from random points located within a similar treatment area surrounding their home range center. Our top model was the same as the above model related to general displacement suggesting a pattern related both to the amount of suitable habitat prior to treatment and the treatment effect, with the former covariate the only significant factor based on confidence limits. Our lower ranked and competing models were similar except that the treatment effect was continuous rather than categorical. Our null model was not competing. Our top model explained slightly less variation than the model relating general home range displacement. We note again our misgivings about the estimation of variation explained by the models given the small sample size. Collectively, we attribute results of this analysis to the same issues discussed above.

Deviations in Implementation of Original Study Design: We designed our study to detect short-term responses (acute effects) of a canopy reduction on spotted owls. This is a key factor that could be related to our general results. As proposed by Verner et al. (1992), desired reduction in fire threats or other modest outcomes of forest management would best be accomplished by a moderate reduction in tree density, reduction in canopy cover, and retention of large trees rather than drastic manipulation of forest structure. Thus, our experimental design followed this general philosophical approach under the guidelines of the modified Sierra Framework (USFS 2004). That is, we expected that owl responses might be modest given moderate rather than drastic changes in forest structure. Indeed, the design of SPLATS was predicated on reducing tree density, ladder fuels, and canopy cover while maintaining large trees.

Our experimental design was based on extensive knowledge of spotted owl ecology gathered by biologists over the last 3 decades. For example, we knew that spotted owls behaved as central place foragers (Carey and Peeler 1995), that they may move nest sites or primary foraging sites over time, and that they show variation among home range size within and among years and geographic areas (Forsman et al. 1984, Carey et al. 1992, Gutiérrez et al. 1995). Hence, we predicted that logical response

variables for evaluating canopy reduction on spotted owls were changes in home range size following a treatment effect (canopy reduction within the owl's HRCA), and shifts or displacements of home ranges in space or relative to the treatment. However, we also predicted that there could be a large number of confounding factors in an experiment such as the extent of treatment, the conditions of the owl's home range prior to treatment (e.g., habitat quality in terms of amount of suitable habitat), natural variation in shifting of territories or use areas within home ranges between years (year effects), timing of treatments (seasonal effects), the social status of the bird, and its breeding status. Thus, we designed our study to reduce the effect of confounding factors as much as possible (e.g., a single season study proposed to reduce year effects) or to model these effects as covariates (e.g., amount of pre-treatment habitat in HRCA). We proposed an experiment that would occur within the same year, have similar treatment extent and type, and have birds that with the same social status (paired). In addition, we selected a random sample of birds from a large population and randomly assigned them to a treatment or control group to broaden our inferential capability, to reduce bias in selection of subjects, and to increase the chance that the study population represented the population as a whole.

The reality of the execution of the original experimental design was that some key failures occurred, which we believe had a substantial influence on the outcome of the study. These deviations from the design are noted as follows and we include them not for punitive, accusatory reasons but because we believe they will help strengthen future studies on adaptive management experiments with spotted owls or other wildlife managed at such a large scale:

1. Initial selection of some areas in owl home ranges could not be logged because of logistical reasons, which required a late assessment of alternative areas. This problem could have been avoided with more careful attention to the criteria set forth for selection of potential sites (i.e., all areas available for selection could be treated).
2. One control site was actually logged. This was a substantial deviation from an experimental design and could have had serious consequences. In view of the imbalance between the number of treated sites and control sites, we switched this 1 site to a "treatment" in an *ad hoc, a posteriori* decision. This had unknown effects on the analysis, but reduced our inferential ability even though we felt it helped with the small sample size issue.
3. The treatment sites were not logged on the proposed scheduled, which necessitated a switch to monitor post-treatment responses the next year. This undoubtedly introduced a confounding year effect. It also resulted in a smaller sample size because birds disappeared over the winter. We felt this was the most serious failure of the implementation of the original design.

In addition to the above failures, the study also suffered from substantial non-demonic intrusions (Hurlbert 1984). That is, we had substantial apparent natural mortality or abandonment of territories between our initial selection of territories and monitoring of resident birds during 2005 and the time we captured birds for radio-marking in spring-summer of 2006. Clearly the absence of these birds was unrelated to transmitters because the birds were not yet radio-marked. Spotted owls also suffered the highest over-winter mortality recorded on the Eldorado demographic study since its inception during this winter (Gutiérrez et al. 2008). Put simply, this was just bad luck in timing of the study. However, we expected some over-winter mortality and account for it

during the design of the study; this over-winter mortality was simply well beyond our expectations so we started our 2006 capture season with a potential study population reduced by 25%. When that low number was coupled with other expected attrition of birds (i.e., inability to capture extremely wary birds, loss of radio contact due to dispersal or transmitter failure, natural mortality after radio-marking), we had only 38% of our maximum proposed study population for the duration of the study.

Management Implications

How do results inform or improve adaptive management relative to SPLATS and spotted owls?: We believe our results demonstrate that radio-telemetry was probably not the best method to assess spotted owl responses to logging (i.e., canopy reduction, SPLATS, etc.). It certainly can be done as we have demonstrated in this study, but there are numerous logistical constraints that impact carefully designed adaptive management experiments. There is also substantial variation in the potential natural responses of owls to changes in habitat use, which can confound the results and would require a much larger sample of radio-marked owls. Our results suggest that such a study might not be financially or logistically feasible at the current time although it is theoretically possible with greater funding and advances in telemetry technology. Our preliminary results from this study led us to recommend an approach based on occupancy analysis (Mackenzie et al. 2006) for the Sierra Nevada Adaptive Management Project, rather than rely on radio telemetry. Occupancy analysis is the evaluation of so-called presence-absence data that is corrected for detection probability. It has the advantage that assessment is based on patch occupancy by owls so that the data are conditional only on an owl having occupied a particular patch at some time. Our recommendation to use occupancy analysis to study chronic effects of SPLATS was accepted by the Sierra Nevada Adaptive Management Project and that decision proved correct based on the final results of this study.

Specific recommendation for adaptive management: We believe that this project was conducted in good faith by all parties involved and that there was extremely good cooperation among interested parties. Personnel of the USFS were helpful and tried to execute the design in a very short time period relative to their normal planning processes. Special provisions were made to issue logging contracts that would deviate from typical harvest time frames in order to facilitate the design. Thus, we feel privileged to have worked with many dedicated professionals to better-understand a long-standing and controversial issue related to spotted owls.

In reviewing various failures, we think there are some important lessons to be learned relative to adaptive management and spotted owls (or any other wildlife species). First, despite our initial good communication, we think communication could be improved. This could be done by forming a specific group of contact persons who would represent each segment of the project (researchers, forest and district biologists, silviculturists, logging engineers, planners, etc.). Such a group should not be unwieldy but rather provide the core contact individuals that would be responsible for elements related to their subject matter. Key individuals would lead discussions and once a decision was made serve as the focal person for execution of that element of the adaptive management project. Second, a list serve or website (closed or open to the public

depending on the project) should be established so that communication could quickly be available to everyone having responsibility on a project. Third, a comprehensive schedule should be developed and posted on this website such that progress on individual components of planning, design execution, field work, and analysis could be monitored to detect potential delays or deviations in a timely manner.

Conclusions

This study demonstrated why no large-scale experiments on the effect of logging on spotted owls have been done using radio-telemetry despite a long-standing desire by biologists to do such experiments (Gutiérrez 1985, Noon and Franklin 2002). It presented substantial logistical, design execution, and planning challenges, which we feel ultimately influenced the results. Yet, it provided a great opportunity to evaluate impediments to success of such experiments. We discovered no single “Achilles Heel” in either our experimental approach or the execution of our design; rather, we encountered a combination of issues that could be dealt with through more carefully planning and design execution. Hence, we did not feel this adaptive management experiment was a failure, but rather a starting point for other studies designed around more robust ways to evaluate the effects of SPLATS on spotted owls and to conduct large-scale experiments in general (e.g., see our “*Specific recommendation for adaptive management*” above). We felt that our models and choice of response variables were appropriate for the techniques we used, but we think that future studies should concentrate on occupancy analysis in conjunction with other demographic parameters based on banded birds because of its expanding potential to jointly estimate multiple states (e.g., occupancy and reproduction) while modeling the outcomes of complex alternatives such as the effect of logging on spotted owls (e.g., MacKenzie et al. In Press), and provide adequate samples sizes for inference in large-scale studies. Moreover, evaluating chronic responses may be more meaningful from both biological and management perspectives because a lack of acute responses does not imply that there are no impact on a species. Rather, negative effects may not manifest themselves for several years. This may be particularly true of spotted owls because they are very long-lived and have very high site fidelity.

ACKNOWLEDGEMENTS

We thank our dedicated and able field assistants who showed a strong, professional commitment to this project: Chris Binchus, Nicole Bygd, Amanda Hover, Rebecca Hundt, Tony Lavictoire, Tom McFarland, Clint Scheuerman, David Wilcox, and Jeff Wright. We thank Vince Berigan for providing logistical and technical advice on GIS and other issues during the entire course of this project and occasional help with field work and John Fieberg for discussing study design during the early stages of planning. We thank Dennis Rock for his advice and guidance on the attachment and use of the radio transmitters. Laura Erickson, Melanie Rossi, and Casey Phillips provided technical support during the study. The University of California’s Blodgett Forestry Center provided field housing and their staff; Sheryl Rambeau, Robert Heald, Robert York, Frieder Schurr, and Russell Seufert were helpful in resolving many issues over the course of the study.

LITERATURE CITED

- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern Spotted Owls, 1985-2003. *Wildlife Monographs* 163.
- Blakesley, J. A., M. E. Seamans, M. M. Conner, A. B. Franklin, G. C. White, R. J. Gutiérrez, J. E. Hines, J. D. Nichols, T. E. Munton, D. W. H. Shaw, J. J. Keane, G. N. Steger, B. R. Noon, T. L. McDonald, and S. Britting. 2006. Demography of the California spotted owl in the Sierra Nevada: report to the U.S. Fish and Wildlife Service on the January 2006 meta-analysis. Colorado State University, Ft. Collins, Colorado, USA.
- Bias, M. A., and R. J. Gutiérrez. 1992. Habitat associations of California spotted owls in the central Sierra Nevada. *Journal of Wildlife Management* 56:584–595.
- Biotas™ (2004). Ecological Software Solutions LLC. Hegymagas, Hungary*. Version 1.03.
- Bond, M. L., M. E. Seamans, and R. J. Gutiérrez. 2004. Modeling nesting habitat selection of California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada using standard forest inventory metrics. *Forest Science* 50:773–780.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag Inc., New York.
- Call, D. R., R. J. Gutiérrez, and J. Verner. 1992. Foraging habitat and home-range characteristics of California spotted owls in the Sierra Nevada. *Condor* 94:880–888.
- Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- Carey, A. B., and K. C. Peeler. 1995. Spotted owls: resource and space use in mosaic landscapes. *Journal of Raptor Research* 29:223–239.
- Chatfield, A. 2005. Habitat selection by a California spotted owl population: a landscape scale analysis using resource selection functions. M.S. Thesis, University of Minnesota, St. Paul, MN.

- Congdon, P. 2003. Applied Bayesian Modelling. John Wiley & Sons Ltd, West Sussex, England.
- Ecological Solutions, 1999. LOAS: Location of a Signal user's guide.
www.ecostats.com.
- Finney, M.A. 2001. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. *Forest Science* 47(2): 219–228.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. U.S.F.S. Gen. Tech. Rep. PNW-GTR-162. Portland, OR.
- Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon . *Wildlife Monographs* 87.
- Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, A. Ellingson, E. C. Meslow, G. S. Miller, K. A. Swindle, J. A. Thraikill, F. F. Wagner, and D. E. Seaman. 2002. Natal and breeding dispersal of northern spotted owls. *Wildlife Monographs* 149.
- Foster, C. C., E. D. Forsman, E. C. Meslow, G. S. Miller, J. Reid, F. F. Wagner, A. B. Carey, and J. B. Lint. 1992. Survival and reproduction of radio-marked adult spotted owls. *Journal of Wildlife Management* 56:91–95.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12–20.
- Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs* 54.
- Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 15-42 *in* Millsaugh, J. J., and J. M. Marzluff (eds.). *Radio tracking and animal populations*. Academic Press, New York.
- Gelman, A. and J. Hill. 2007. *Data Analysis using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, USA
- Gutiérrez, R. J. 1985. Information and research needs for spotted owl management. In R. J. Gutiérrez and A. B. Carey (eds.). *Ecology and management of spotted owls in the Pacific Northwest*. U.S.D.A. Pacific Northwest Forest and Range

- Experiment Station. Gen. Tech. Rep. PNW 185:115–118.
- Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Stix occidentalis*). In A. Poole and F. Gill (eds.). The Birds of North America No. 179. Life Histories for the 21st Century. The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D.C.
- Gutiérrez, R. J., A. B. Franklin, W. S. LaHaye, V. J. Meretsky, and J. P. Ward. 1985. Juvenile spotted owl dispersal in northwestern California: preliminary results. In R. J. Gutiérrez and A. B. Carey (eds.). Ecology and management of spotted owls in the Pacific Northwest. U.S. Department of Agriculture, Forest Service General Technical Report PNW 185:60–65.
- Gutiérrez, R. J., J. Verner, K. S. McKelvey, B. R. Noon, G. S. Steger, D. R. Call, W. S. LaHaye, B. B. Bingham, and J. S. Senser. 1992. Habitat relations of the California spotted owl. Pages 79-147. In J. Verner et al. (eds.). The California spotted owl: a technical assessment of its current status. U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.
- Gutiérrez, R. J., and D. J. Tempel. 2008. Population ecology of the California spotted owl in the central Sierra Nevada: annual report 2007. Unpublished project report, U.S. Forest Service, Region 5, Vallejo, California.
- Hooge, P. N. and B. Eichenlaub. 1997. Animal movement extension to arcview. ver. 1.1. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.
- Horne, J. S., and E. O. Garton. 2006a. Animal Space Use 1.0 Beta. <http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm>. Accessed 09 Nov 2006.
- Horne, J. S., and E. O. Garton. 2006b. Selecting the best home range model: an information theoretic approach. *Ecology* 87:1146–1152.
- Horne, J. S., and E. O. Garton. 2006c. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home range analysis. *Journal of Wildlife Management* 70:641–648.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Irwin, L. L., Clark, L. A., D. C. Rock, and S. L. Rock. 2007. Modeling foraging habitat of California spotted owls. *Journal of Wildlife Management* 71:1183–1191.
- Jennings, S. B., N. B. Brown, and N. Schiel. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures.

- Forestry 72:59–74.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling, inferring patterns and dynamics of species occurrence. Elsevier, Oxford, UK.
- MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. In Press. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology.
- Moen, C. A., Franklin, A. B., and R. J. Gutiérrez. 1991. Age determination of subadult northern spotted owls in northwest California. Wildlife Society Bulletin 19:489–493.
- Moen, C. A., and R. J. Gutiérrez. 1997. California spotted owl habitat selection in the central Sierra Nevada. J. Wildlife Management 61:1281–1287.
- Moen, C. A., Franklin, A. B., and R. J. Gutiérrez. 1991. Age determination of subadult northern spotted owls in northwest California. Wildlife Society Bulletin 19:489–493.
- Noon, B. A., and A. B. Franklin. 2002. Scientific research and the spotted owl (*Strix occidentalis*): opportunities for major contributions to avian population ecology. Auk 119:311–320.
- Paton, P. W. C., C. J. Zabel, D. L. Neal, G. N. Steger, N. G. Tilghman, and B. R. Noon. 1991. Effects of radio tags on spotted owls. Journal of Wildlife Management 55:617–622.
- Reynolds, R. T., G. C. White, S. M. Joy, and R. W. Mannan. 2004. Effects of radio transmitters on Northern Goshawks: do tail mounts lower survival of breeding males? Journal of Wildlife Management 68:25–32.
- Seamans, M. E., R. J. Gutiérrez, C. May, and M. Z. Peery. 1999. Demography of two Mexican spotted owl populations. Conservation Biology 13:744–754.
- Seamans, M. E., R. J. Gutiérrez, C. A. Moen, and M. Z. Peery. 2001. Spotted owl demography in the central Sierra Nevada. Journal of Wildlife Management 65:425–431.
- Seamans, M. E., and R. J. Gutiérrez. 2007. Habitat selection in a changing environment: the relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. Condor 109:566–576.
- Seamans, M. E., and R. J. Gutiérrez. 2007. Population ecology of the California spotted owl in the central Sierra Nevada: annual results 2006. Unpublished project report,

- U.S. Forest Service, Region 5, Vallejo, California.
- Simberloff, D. 1987. The spotted owl fracas: mixing academic, applied, and political ecology. *Ecology* 68: 766–772.
- SNEP (Sierra Nevada Ecosystem Project). 1996. Status of the Sierra Nevada: assessment summaries and management strategies. Volume 1. Wildland Resources Center Report No. 36, University of California, Davis.
- Spiegelhalter, D. J., A. Thomas, N. G. Best, and D. Lunn. 2003. WinBugs Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge, UK.
- Tempel, D. J., and R. J. Gutiérrez. 2003. Fecal corticosterone levels in California spotted owls exposed to low-intensity chainsaw sound. *Wildlife Society Bulletin* 31:698–702.
- Tempel, D., and R. J. Gutiérrez. 2004. Factors related to fecal corticosterone levels in California Spotted Owls: implications for assessing chronic stress. *Conservation Biology* 18:538–547.
- U.S. Fish and Wildlife Service. 2003. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the California spotted owl (*Strix occidentalis occidentalis*). *Federal Register* 68:7580–7608.
- U. S. Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants: 90-day finding on a petition to list the California spotted owl as threatened or endangered. *Federal Register* 70:35607–35614.
- U.S. Fish and Wildlife Service. 2006. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the California spotted owl (*Strix occidentalis occidentalis*) as threatened or endangered. *Federal Register* 71:29886–29908.
- U.S. Forest Service. 1993. California spotted owl Sierran Province interim guidelines environmental assessment, decision notice, and findings of no significant impact. USDA Forest Service. Pacific Southwest Region. San Francisco, California, USA.
- U.S. Forest Service. 1996. Revised Draft Environmental Impact Statement: managing California spotted owl habitat in the Sierra Nevada National Forests of California, an ecosystem approach. USDA Forest Service. Pacific Southwest Region. San Francisco, California, USA.
- U.S. Forest Service. 2001. Sierra Nevada Forest Plan Amendment: Final Environmental Impact Statement Volumes 1–6. Pacific Southwest Region. Vallejo, CA.

- U.S. Forest Service. 2004. Sierra Nevada Forest Plan Amendment: Final Supplemental Environmental Impact Statement. Volumes 1–4. Pacific Southwest Region, Vallejo, CA.
- Verner, J. 1992. Data needs for avian conservation biology: have we avoided critical research? *The Condor* 94: 301–303.
- Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould Jr, and T. W. Beck. 1992. The California spotted owl. a technical assessment of its current status. US Forest Service, Pacific Southwest Research Station General Technical Report, Berkeley, CA.
- Ward, J. P. Jr., R. J. Gutiérrez, and B. R. Noon. 1998. Habitat selection by northern spotted owls: the consequences of prey selection and distribution. *Condor* 100:79-92.
- Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068.

Table 1. Equations used to estimate tree and stand basal areas used as covariates to assess treatment effects when reducing canopy cover in spotted owl territories in the central Sierra Nevada, California 2005–2007.

Metric	Equation	Explanation
BA (ft ²)	$\text{PI} * (\text{dbh}/2)^2$	$\text{Pi } r^2$
Stand BA (ft ² /ac) for small trees in 0.1213ac plot	$\sum \text{BA} / 17.467$	17.467 was derived by multiplying .1213 (size of plot in acres) by 144 (conversion factor for in. to ft.)
Stand BA (ft ² /ac) for large trees in 0.4852ac plot	$\sum \text{BA} / 69.869$	Same as above, except plot size is .4852 ac
Density (#/ac) for small trees	$N / 0.1213$	Number of trees divided by the plot size
Density (#/ac) for large trees	$n/0.4852$	Number of trees divided by the plot size
All snag measurements were calculated the same as the live tree measurements above		

Table 2. A priori models designed to evaluate the effect of canopy cover reduction on California spotted owls in the central Sierra Nevada, California, 2006–2007.

Response = Home range size change (ΔHR)

Model No.	Model Description	Model Variables ^a and Predictions ^b
1	Treatment/Control (T: Treatment = 1 control = 0)	$\Delta HR = B_0 + B_1 * T$
2	Treatment area	$\Delta HR = B_0 + B_1 * TA$
3	Treatment/Control + pre-treatment spotted owl habitat	$\Delta HR = B_0 + B_1 * T + B_2 * SOH$
4	Treatment area + pre-treatment spotted owl habitat	$\Delta HR = B_0 + B_1 * TA + B_2 * SOH$
5	Pre-treatment canopy closure and treatment area effect	$\Delta HR = B_0 + B_1 * CC + B_2 * TA$
6	Pre-treatment large tree density and treatment area effect	$\Delta HR = B_0 + B_1 * LTD + B_2 * TA$
7	Means	$\Delta HR = B_0$

Response = Change in home range centroid (Δ CENT)

Model No.	Model Description	Model Variables ^a and Predictions ^b
1	Treatment/Control (T: Treatment =1 control = 0)	Δ CENT = $B_0 + B_1 * T$
2	Treatment area	Δ CENT = $B_0 + B_1 * TA$
3	Treatment/Control + Spotted owl Habitat (area of habitat pre-treat or post)	Δ CENT = $B_0 + B_1 * T + B_2 * SOH$
4	Treatment area + Spotted owl Habitat pre-treatment	Δ CENT = $B_0 + B_1 * TA + B_2 * SOH$
5	Pre-treatment canopy closure and treatment effect	Δ CENT = $B_0 + B_1 * CC + B_2 * TA$
6	Pre-treatment large tree density and treatment effect	Δ CENT = $B_0 + B_1 * LTD + B_2 * TA$
7	Means	Δ CENT = B_0

All models above are described in narrative form below, and are the same models for all three response variables. In addition, the predicted response is the same for all response variables because we hypothesized that increase in home range size and increases in displacement distances between pre and post treatment centroids would reflect a negative response (i.e., the smaller the home range and the less a bird moves the better).

Model 1: Treatment birds (regardless of treatment area) increased their home range size/centroid distance more than control birds.

Model 2: Birds with a greater area treated increased their home range or centroid distance more than birds with less area treated (included control birds that had no area treated).

Model 3: Birds with more spotted owl habitat during the pre-treatment period would be less likely to increase their home range size or centroid distance than birds with less spotted owl habitat (if SOH habitat were on the x-axis and home range or centroid distance on the y-axis, you would see a decreasing line – the additive effect would

actually result in 2 decreasing parallel lines, with treatment birds having larger home range changes or centroid distance at all values of SOH than control birds).

Model 4: This is similar to model 3 (same predictions) except that the Treatment effect variable is continuous rather than categorical – therefore, instead of having two decreasing lines on the graph I described above, you would have a response surface.

Model 5: Birds with lower canopy closure during the pre-treatment period would have larger increases in home range size or centroid distance; at the same time, birds with more area treated would have larger increases in home range size than control birds or birds with smaller areas treated.

Model 6: Birds with lower density of large trees during the pre-treatment period would have larger increases in home range size or centroid distance; at the same time, birds with more area treated would have larger increases in home range size than control birds or birds with smaller areas treated.

Model 7: Home range size or the position of the home range did not change between the pre and post treatment period.

Table 3. Summary of survey effort, status, and fate of spotted owl randomly selected for experimental study on the effects of canopy reduction in the central Sierra Nevada, California, 2005–2007.

Original Site ¹	Sex	Experimental Unit	# Surveys 2005 ²	2005 Status ³	Fate 2006/7 ⁴
Bald Mountain	F	Control	13	Pair	K
Bald Mountain	M	Control	13	Pair	S (n = 3, 23)
Canyon Creek	M	Treatment	18	Pair	S (n = 6, 4)
Canyon Creek	F	Treatment	18	Pair	ND
Dixie Queen Mine	F	Control	8	Pair	S (n = 2, *)
Dixie Queen Mine	M	Control	8	Pair	ND
Dolly	F	Treatment	10	Pair	FM
Dolly	M	Treatment	10	Pair	F
ED028	F	Control	9	Pair	S (n = 2, 1)
ED028	M	Control	9	Pair	S (n = 2, 4)
ED059	F	Control	11	Pair	NA
ED059	M	Control	11	Pair	NA
ED121	F	Treatment (replacement site)	4	Pair	S (n = 5, 2)
ED121	M	Treatment (replacement site)	4	Pair	F
ED124	F	Treatment (originally control, replaced as treatment site)	7	Pair	S (n = 3, 1)
ED124	M	Treatment (originally control, replaced as treatment site)	7	Pair	FM
ED164	F	Treatment	14	Pair	NA
ED164	M	Treatment	14	Pair	NA
ED200	F	Control (replacement site)	6	None	FM
ED200	M	Control (replacement site)	6	Single	ND
Long Meadow	F	Treatment	7	Pair	ND
Long Meadow	M	Treatment	7	Pair	ND
Rob's Peak	F	Control	21	Pair	ND
Rob's Peak	M	Control	21	Pair	S (n = 7, 14**)
Sugar	F	Treatment (originally control)	7	Pair	D
Sugar	M	Treatment (originally control)	7	Pair	S (n = 3, 1)
Whiskey	F	Treatment	15	Pair	ND
Whiskey	M	Treatment	15	Pair	ND

Original Site¹: these are all the original 24 birds plus replacement territories selected for the study. Names are either geographic place names or alpha-numeric designators for territories assigned by agencies.

Surveys 2005²: the number of surveys conducted within a territory to estimate occupancy of birds at that site.

2005 Status³: either pair or single bird detected at territory (no territories were surveyed inadequately to determine occupancy status except replacement territories in year 2005).

Fate⁴: the presumed fate of the birds detected at any time during the study designated as follows:

S = successfully monitored for the course of the study or we gained sufficient information to include in study (n = x, y) where x = the number of surveys conducted in 2006 to find and radio mark birds; y = number of surveys in 2007 and 2008 to capture and remove radios for that bird. Surveys include both night and day walk-in surveys. * = We collected enough information from this bird, but bird was found dead near end of monitoring period and thus was not recaptured to remove radio transmitter, cause of death unknown. ** = Bird died over winter, recovered in spring 2008 after snow melt. Cause of death unknown.

ND = Detected during 2005 surveys but not detected during 2006 surveys to locate and radio mark owls (i.e., bird either died or dispersed over winter)

F = Failure to capture

FM = Bird captured and radio marked, but we failed to monitor it adequately because it dispersed onto private land (no access), its radio failed, or it disappeared for unknown reasons.

D = Died, cause unknown

K = Killed by vehicle on highway

NA = Not applicable. These were birds that were initially selected for the study, but were later dropped from the study because the USFS could not treat sites for logistical reasons (too steep).

Table 4. Summary of monitoring and transmitter attachment periods and number of locations derived during pre- and post-treatment experimental periods for the effect of canopy cover on spotted owls in the central Sierra Nevada, 2006–2007.

Bird ¹	Monitor Period ²	Radio Period ³	Pre-treat loc ⁴	Post treat loc ⁵
Bald Mountain (C, M)	443	798	79	62
Canyon Creek (T, M)	409	437	66	95
Dixie Queen (C, F)	415	449	67	67
ED028 (C, F)	427	461	65	61
ED028 (C, M)	427	469	54	68
ED121 (T, F)	402	437	92	85
ED124 (T, F)	426	475	105	60
Rob's Peak (C, M)	399	693	95	109
Sugar (T, M)	442	468	95	138

¹Bird: the Territory name, experimental category, and sex of owl (C = control site and T = treatment site; F = female and M = male)

²Monitor Period: the period of time over which we actively gathered radio telemetry locations

³Radio Period: the period of time over which the bird carried a transmitter whether or not it was being monitored.

⁴Pre-treat loc: The number of usable radio telemetry locations derived during the 2006 pre-treatment period.

⁵Post-treat loc: the number of usable radio telemetry locations derived during the 2007 post-treatment period.

Table 5. Comparison of home range estimators using pre-treatment radio telemetry locations for California spotted owls in the central Sierra Nevada, California 2006–2007 using Animal Space Use software. Locations have confidence ellipses ≤ 18.5 ac and are from nighttime and daytime surveys (including dusk, night, dawn, and day period roosts).

Site	Sex	EC ¹	Home Range Model	# Parameters	AICc ²	CVC ³
BALDM	M	C	Adaptive Kernel Density	NA	NA	2277.08
BALDM	M	C	Fixed Kernel Density	NA	NA	2284.26
BALDM	M	C	2 Mode Bivariate Normal	11	2317.71	2317.77
BALDM	M	C	2 Mode Bivariate Circle	7	2358.50	2357.52
BALDM	M	C	1 Mode Bivariate Normal	6	2389.96	2388.44
BALDM	M	C	Exponential Power Model	4	2517.41	2516.11
CANYC	M	T	Adaptive Kernel Density	NA	NA	1921.81
CANYC	M	T	Fixed Kernel Density	NA	NA	1934.63
CANYC	M	T	2 Mode Bivariate Circle	7	1993.01	1986.97
CANYC	M	T	2 Mode Bivariate Normal	11	1990.58	1990.51
CANYC	M	T	1 Mode Bivariate Normal	6	2036.77	2035.19
CANYC	M	T	Exponential Power Model	4	2076.69	2075.93
DIXQM	F	C	Adaptive Kernel Density	NA	NA	1876.28
DIXQM	F	C	Fixed Kernel Density	NA	NA	1902.37
DIXQM	F	C	2 Mode Bivariate Normal	11	2012.14	2011.37
DIXQM	F	C	2 Mode Bivariate Circle	7	2060.28	2057.65
DIXQM	F	C	1 Mode Bivariate Normal	6	2060.65	2065.78
DIXQM	F	C	Exponential Power Model	4	2172.68	2169.71
ED028	F	C	Adaptive Kernel Density	NA	NA	1809.81
ED028	F	C	Fixed Kernel Density	NA	NA	1811.35
ED028	F	C	2 Mode Bivariate Circle	7	1826.96	1824.40
ED028	F	C	2 Mode Bivariate Normal	11	1818.07	1832.48
ED028	F	C	1 Mode Bivariate Normal	6	1863.21	1887.33
ED028	F	C	Exponential Power Model	4	1904.31	1917.29
ED028	M	C	Fixed Kernel Density	NA	NA	1536.11
ED028	M	C	Adaptive Kernel Density	NA	NA	1538.46
ED028	M	C	2 Mode Bivariate Normal	11	1551.89	1559.72
ED028	M	C	2 Mode Bivariate Circle	7	1583.35	1581.57
ED028	M	C	Exponential Power Model	4	1598.80	1597.12
ED028	M	C	1 Mode Bivariate Normal	6	1598.08	1600.22
ED121	F	T	Adaptive Kernel Density	NA	NA	2693.86
ED121	F	T	Fixed Kernel Density	NA	NA	2695.99
ED121	F	T	2 Mode Bivariate Normal	11	2724.82	2725.11
ED121	F	T	2 Mode Bivariate Circle	7	2745.29	2743.68
ED121	F	T	1 Mode Bivariate Normal	6	2793.70	2798.68
ED121	F	T	Exponential Power Model	4	2846.50	2847.88
ED124	F	T	Fixed Kernel Density	NA	NA	3125.38
ED124	F	T	Adaptive Kernel Density	NA	NA	3128.19
ED124	F	T	2 Mode Bivariate Normal	11	3270.82	3270.22
ED124	F	T	2 Mode Bivariate Circle	7	3312.12	3281.38
ED124	F	T	1 Mode Bivariate Normal	6	3328.58	3332.95
ED124	F	T	Exponential Power Model	4	3360.89	3359.74
ROBPK	M	C	Adaptive Kernel Density	NA	NA	2706.90

ROBPK	M	C	Fixed Kernel Density	NA	NA	2718.23
ROBPK	M	C	2 Mode Bivariate Circle	7	2747.42	2750.29
ROBPK	M	C	2 Mode Bivariate Normal	11	2744.05	2753.78
ROBPK	M	C	1 Mode Bivariate Normal	6	2748.61	2754.59
ROBPK	M	C	Exponential Power Model	4	2817.35	2793.23
SUGAR	M	T	Adaptive Kernel Density	NA	NA	2581.68
SUGAR	M	T	Fixed Kernel Density	NA	NA	2587.08
SUGAR	M	T	1 Mode Bivariate Normal	6	2646.02	2646.84
SUGAR	M	T	2 Mode Bivariate Normal	11	2638.19	2656.68
SUGAR	M	T	2 Mode Bivariate Circle	7	2733.97	2738.93
SUGAR	M	T	Exponential Power Model	4	2869.09	2866.30

¹ EC – Experimental category (C=control, T=treatment)

² AICc = Akaike's information criterion corrected for small sample size

³ CVC = Likelihood cross-validation criterion

Table 6. Habitat characteristics and treatment areas for experimental reduction of canopy cover within spotted owl territories in the central Sierra Nevada, 2006–2007.

Site	EC ¹	TA ²	CCPRE ³	CCPOST ⁴	LTDPRE ⁵	LTDPOST ⁶	PSH ⁷	PCSH ⁸
BALDM M	C	0	90.5	90.5	12.5	12.5	70.9	2.0
CANYC M	T	240.5	81.7	68.6	6.1	7.1	36.9	-25.5
DIXQM F	C	0	68.2	68.2	5	5	29.3	47.2
ED028 F	C	0	67.1	67.1	10.8	10.8	38.8	8.5
ED028 M	C	0	67.1	67.1	10.8	10.8	39.9	1.5
ED121 F	T	321.0	59.4	49.4	17	12.4	19.0	14.3
ED124 F	T	271.4	56.5	43.5	8.8	7.2	34.0	65.0
ROBPK M	C	0	73.8	73.8	14	14	13.2	32.1
SUGAR M	T	82.4	90.3	59.7	14.7	14.4	53.2	-2.5

EC¹: Experimental unit (C=control, T=treatment)

TA²: Total area treated to reduce canopy (ac)

CCPRE³: Pre-treatment average percent canopy cover. All canopy cover estimates were during field sampling using a densitometer except the pre-treatment canopy cover estimate for the Sugar Territory male, which was estimated from vegetation surveys taken from the pre-treatment kernels of the Sugar Territory male. The latter estimate was necessary because the area was originally a control but was logged (see discussion regarding these measurements).

CCPOST⁴: Post-treatment average percent canopy cover

LTDPRE⁵: Pre-treatment large-tree density (# trees/ac)

LTDPOST⁶: Post-treatment large tree density (# trees/ac)

PSH⁷: Proportion of suitable habitat in owl home range prior to treatment

PCSH⁸: Percent change in suitable habitat within owl home range as a result of treatment

Table 7. Estimated response variables for individual California spotted owls in the central Sierra Nevada, CA, 2006–2007, undergoing canopy reduction in their home ranges.

Site	Sex	EC ¹	Pre- HR ²	Post- HR ³	CHR ⁴	GD ⁵	GT ⁶
BALDM	M	C	403.7	837.3	433.6	30806	30173
CANYC	M	T	356.9	1125.5	768.6	11093	8539
DIXQM	F	C	285.0	442.9	158.0	26796	22393
ED028	F	C	249.9	400.8	150.9	1282	262
ED028	M	C	459.1	673.5	214.3	612	-412
ED121	F	T	455.4	175.4	-280.0	629	-361
ED124	F	T	582.0	362.6	-219.4	41414	40798
ROBPK	M	C	413.8	413.4	-0.4	5426	338
SUGAR	M	T	133.9	318.0	184.2	1228	-945

EC¹: Experimental category (C=control, T=treatment)

Pre- HR²: Pre-treatment 95% adaptive kernel (area in acres)

Post- HR³: Post-treatment 95% adaptive kernel (area in acres)

CHR⁴: Change in home range size between pre- and post-treatment (area in acres)

GD⁵: General home range displacement, which is the distance between the centroid of all pre-treatment locations within the 95% adaptive kernel estimate and the centroid of all post-treatment locations within the 95% adaptive kernel estimate (distance in feet)

GT⁶: General home range displacement is relative to treatment; which was calculated as pre-treatment distance between the centroid and the treatment plot (or random point for control territories) minus the post-treatment distance between the new post-treatment centroid and the original treatment location or original random location, if a control (distance in feet).

Table 8. Bayesian model selection results for three response variables assessing the effect of canopy reduction on California spotted owls in the central Sierra Nevada, California, 2006–2007.

Model	Model Variables and Predictions	Dbar	PD	DIC	Delta DIC
<u>Response Variable: Difference in Home Range Size¹</u>					
Pretreatment canopy closure and treatment area effect	$\Delta HR = B_0 - B_1 * CC + B_2 * TA$	127.090	4.118	131.207	0.000
Means Model	$\Delta HR = B_0$	130.424	2.129	132.553	1.346
Treatment area	$\Delta HR = B_0 + B_1 * TA$	131.143	3.323	134.466	3.259
Treatment/Control + pretreatment spotted owl habitat	$\Delta HR = B_0 + B_1 * T - B_2 * SOH$	130.303	4.348	134.651	3.444
Treatment area + pretreatment spotted owl habitat	$\Delta HR = B_0 + B_1 * TA - B_2 * SOH$	130.297	4.413	134.710	3.503
Treatment/Control (T: Treatment =1 control = 0)	$\Delta HR = B_0 + B_1 * T$	131.549	3.228	134.777	3.570
Pretreatment large tree density and treatment area effect	$\Delta HR = B_0 - B_1 * LTD + B_2 * TA$	130.432	4.385	134.817	3.610
<u>Response Variable: Owl Movement following treatment (Centroid-Centroid Difference)²</u>					
Treatment/Control + Spotted owl Habitat (area of habitat pretreat or post)	$\Delta CENT = B_0 + B_1 * T - B_2 * SOH$	200.034	2.160	202.193	0.000
Treatment area + Spotted owl Habitat pretreatment	$\Delta CENT = B_0 + B_1 * TA - B_2 * SOH$	200.826	3.313	204.139	1.946
Pretreatment canopy closure and treatment effect	$\Delta CENT = B_0 - B_1 * CC + B_2 * TA$	201.991	3.333	205.324	3.131
Means model	$\Delta CENT = B_0$	204.487	1.024	205.510	3.317
Treatment/Control (T: Treatment =1 control = 0)	$\Delta CENT = B_0 + B_1 * T$	204.474	1.042	205.516	3.323
Treatment area	$\Delta CENT = B_0 + B_1 * TA$	203.379	2.181	205.560	3.367
Pretreatment large tree density and treatment effect	$\Delta CENT = B_0 - B_1 * LTD + B_2 * TA$	203.420	2.897	206.316	4.123
<u>Response Variable: Owl Movement (Centroid-Treatment) Relative to Treatment³</u>					

Treatment/Control + Spotted owl Habitat (area of habitat pretreat or post)	$\Delta\text{CENT} = B_0 + B_1 * T - B_2 * \text{SOH}$	199.913	2.160	202.073	0.000
Treatment area + Spotted owl Habitat pretreatment	$\Delta\text{CENT} = B_0 + B_1 * \text{TA} - B_2 * \text{SOH}$	200.739	3.313	204.052	1.979
Means model	$\Delta\text{CENT} = B_0$	203.466	1.029	204.495	2.422
Treatment/Control (T: Treatment =1 control = 0)	$\Delta\text{CENT} = B_0 + B_1 * T$	203.456	1.048	204.504	2.431
Treatment area	$\Delta\text{CENT} = B_0 + B_1 * \text{TA}$	202.551	2.185	204.736	2.663
Pretreatment canopy closure and treatment effect	$\Delta\text{CENT} = B_0 - B_1 * \text{CC} + B_2 * \text{TA}$	202.136	3.333	205.469	3.396
Pretreatment large tree density and treatment effect	$\Delta\text{CENT} = B_0 - B_1 * \text{LTD} + B_2 * \text{TA}$	202.987	2.911	205.899	3.826

¹Change in home range size between pre- and post-treatment

²Change in home range center (as defined by the center of all telemetry locations pre- and post-treatment)

³Change in home range center (as defined by the center of all telemetry locations pre- and post-treatment) relative to the either a treatment (for treatment birds) or a random point with the HRCA (for control birds)

Appendix 1. Chronological history of spotted owls randomly selected for study on the effects of canopy reduction on home range size and HRCA displacement (Territory names are either geographic place names or agency alpha-numeric identification numbers for the site).

Canyon Creek Territory - Female

We recorded two vocal detections at night of a female at Canyon Creek in 2005 (26 July and 9 August) during 18 surveys. She was in the vicinity of a vocalizing male, but we did not detect this female visually. We did not detect the Canyon Creek male with a female again until 2007, after he had moved to a different HRCA.

Canyon Creek Territory - Male

We first detected this bird on 21 June 2005, during our 5th survey of this territory. We established by protocol (see Seamans 2005) that the bird was not nesting on 3 August 2005. We continued to monitor this bird in 2005 using standard surveys, which consisted of 9 non-detection surveys and 9 walk-in (detection) surveys. In 2006, we located him during a walk-in survey on 2 May, but did not capture him until our 6th walk-in survey and capture attempt on 12 June. This bird was elusive in both 2005 and 2006, which is supported by the following observations. We believe that he was single for the entire 2006 field season because we never detected a female near him. He made some wide-ranging movements in September and October 2006, during which time he was difficult to monitor. He disappeared after 22 August and, despite our many nights of ground search, we were unsuccessful in finding him until we monitored his radio signal from the air during an aerial search on 18 September. We located this bird during a subsequent ground search approximately 11 km (6.9 miles) from his original location.

In 2007, he appeared to have established a territory near Little Silver Creek, which was approximately 3.2 km (2 miles) west of his original location. On our first visit on 5 April, he was accompanied by a female, who stayed with him all season. We established by protocol that this pair was not nesting on 1 June. During 2007, we consistently found him roosting in the Little Silver Creek area. For this bird we collected 66 pre-treatment locations and 163 post-treatment locations. After 4 walk-in attempts, we removed his radio on 23 August 2007. This bird wore its transmitter for 437 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

Bald Mountain Territory - Female

We detected this bird with a male (presumed mate) on our first visit to Bald Mountain on 6 April 2005. We determined using standard protocol during later visits that this pair was not nesting in 2005. In 2006, we captured the pair and attached radio transmitters on our third walk-in survey on 5 May. We successfully monitored her for several nights until we recovered her body on Wentworth Springs Road on 5 August 2006. She was apparently hit by a vehicle during the night.

Bald Mountain Territory - Male

We detected this bird with a female (presumed mate) on our first visit to Bald Mountain on 6 April 2005. We determined using standard protocol during later visits that this pair

was not nesting in 2005. In 2006, we captured the pair and attached radio transmitters on our third walk-in survey on 5 May. We radio monitored him consistently on Bald Mountain until we no longer could detect his signal after 31 August 2006. After 7 thorough searches of the area using vehicle to monitor from strategic locations, we located his signal on 13 September from Darling Ridge Road, approximately 6.5 km (4 miles) to the west of his territory at Bald Mountain. For the duration of the 2006 field season, we monitored him with some difficulty. His activity consisted of large roaming movements along a 5.6 km (3.5 mile) stretch of Darling Ridge Road, from which there were limited public access roads to allow adequate monitoring coverage. On 25 April 2007 we located him with a new female during a walk-in survey. For most of May, it was almost impossible to get valid locations on him because we think he was usually on a parcel of private land that had rugged topography and no road access, which did not allow radio monitoring of his transmitter signal. In early June, he moved to an area that was slightly more conducive to radio telemetry and we were better able to monitor his movements. This bird displayed an impressive ability to elude recapture. During the fall of 2007, this bird alternated between roosting on (inaccessible) private land and roosting on public land. We had 13 occasions in the fall of 2007 when we could access this bird and he would flush and fly out of sight when we approached. We finally caught him after 23 capture attempts starting in August 2007 and ending on 15 July 2008; we removed his radio at that time. We collected 79 pre-treatment locations, and 113 post-treatment locations for this bird. This bird wore its transmitter for 798 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

Dixie Queen Mine Territory - Female

On 27 May 2005, we detected a pair at Dixie Queen Mine, and on 6 June we determined that they were nesting. This territory was part of the Eldorado regional study area and the birds were already banded to facilitate individual identification (Seamans 2005). We confirmed during 5 follow-up surveys that their nesting attempt had failed. On 25 May 2006, she was with a male that we did not detect again. On 25 May and on 5 June we established, by protocol, that she did not nest in 2006. We captured and outfitted her with a radio transmitter on 5 June. From June-August 2006, she moved frequently between Duncan Canyon and the Middle Fork American River Canyon; during this time she was often located in the wildfire-burned area below Red Star Ridge. We had difficulty getting valid telemetry locations for her, as well as locating her during walk-ins when she was in the burned area because we think she was roosting and foraging deep in these canyons beyond reliable telemetry monitoring. In fall 2006, she moved even more, spending substantial time on Ralston Ridge, as well as exhibiting apparent exploratory movements to areas 5 km (3.1 miles) to the west and 8 km (5 miles) to the east, the latter area near Hellhole Reservoir. She returned to Red Star Ridge and Ralston Ridge during October 2006. During these extensive movements, the data has a few gaps in continuous telemetry monitoring, which was indicative of the difficulty in relocating a bird that relocates frequently or uses inaccessible sites. In 2007, she appeared to have settled with a mate at a historic demography site we termed Spillway, near Hellhole Reservoir. We were able to establish that she did not nest in 2007 and she was consistently located within this territory. However, there were several nights that we had few reliable

telemetry locations. We suspect that she was deep in the canyon during these events, which precluded reliable signal monitoring because of the limited access and steep, rocky terrain. We collected 67 pre-treatment locations, and 96 post-treatment locations for this bird. Our last monitoring date for her was 25 July. On 28 August 2007 we recovered her remains of her body from near her territory. This bird wore its transmitter for 415 monitoring days (her transmitter was still active when we found her remains at 449 days post-radio marking) during which time the signal strength was good throughout the time we monitored her. She appeared healthy on our last walk-in visit to her site on 12 July, 2007. We believe that she must have died at least a couple of weeks before we found her because there were only remnants of her body and feathers, which did not allow speculation on the cause of death. Thus, we could not send in her body for necropsy.

Dixie Queen Mine Territory - Male

On 5 June 2005, we detected a nesting pair at Dixie Queen Mine. Our 5 follow-up visits confirmed that their nest had failed. This pair had been banded previously as part of our Eldorado demographic study so we knew the identities of these birds. Our first of 8 surveys in 2006 revealed a new male (this male was not captured), but this was the only time a male was detected within this territory in 2006. We believe the female was single for all of 2006.

Dolly Territory - Female

We detected a pair at Dolly Territory on 30 May 2005, which we subsequently visited 9 times during the field season to determine that they were not nesting. In 2006, we captured the female on our 6th visit to the site on 8 June. We successfully monitored the female through the end of October in 2006. At times she was difficult to locate because she would enter a wilderness area where there was no road access. However, we were able to record 156 usable locations by the end of October. In the spring of 2007, we could not locate either member of the pair. We conducted 7 night surveys and several mobile searches by vehicle using an omni-directional antenna mounted on the vehicle. We searched for her from the air on 31 May. On 13 August we discovered 2 juveniles at this site. We detected a female on 16 August and 28 August. We were unable to get close enough to her to identify her. After we detected the female, we surveyed the area 3 more times, and did not detect her. Since we were not able to collect any data on this bird in 2007, we did not use her in the analysis. This bird wore its transmitter for at least 140 days before we lost her signal; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., obvious signs of transmitter irritation indicated by excessive preening or pulling of transmitter harness). In 2008, we captured an unbanded female at Dolly Territory, who was paired with a male of unknown origin. This could have been the same female from 2007, but we were uncertain because we were not able to identify the female in 2007.

Dolly Territory - Male

We detected a pair of birds at Dolly Territory on 30 May 2005, which we subsequently visited 9 times that season and we determined that they were not nesting. In 2006, we were unable to capture this uncooperative male. He did not show any interest in mice, and would usually fly out of sight whenever an observer came within 25 meters of him.

We visited this site 14 times with the intention of capturing him, including 8 surveys when we detected him and 6 surveys when we did not detect him. Thus, this bird was not included in the study.

ED028 Territory - Female

In 2005, we surveyed ED028 Territory 9 times during which we recorded 8 detections, including one during which we located a fledgling. On our second capture attempt visit on 25 May 2006, we captured both birds and attached radio transmitters. We were able to successfully monitor and record telemetry locations from this female regularly throughout the length of the study. She was normally located in a drainage near the HRCA center. We collected 65 pre-treatment locations, and 86 post-treatment locations for this bird. In 2007, we recaptured her on our first attempt on 29 August and removed her transmitter. This bird wore its transmitter for 461 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

ED028 Territory - Male

In 2005, we surveyed ED028 Territory 9 times during which we recorded 8 detections, including one during which we located a fledgling. On our second capture attempt visit on 25 May 2006, we captured both birds and attached radio transmitters. We typically found the male near the female and mainly foraging on either side of the main drainage in their territory. He sometimes ventured into a drainage to the east, as well as to the north in an area above our road access. Although there were several nights when we could not locate him, we were usually able to record at least a couple of detections every week. We had some gaps between recorded locations because of a lack of road access to the north of his usual foraging area and because he made a few atypical movements that were difficult to follow. We collected 54 pre-treatment locations, and 112 post-treatment locations for this bird. After 4 attempts, we recaptured him and removed his radio on 6 September. This bird wore its transmitter for 469 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

ED121 Territory - Female

After ED121 Territory was randomly selected as a “replacement” site in late 2005, we visited the territory 4 times. We determined that the site contained a pair, but we were not able to establish reproductive status for the pair because they were quite uncooperative and shy of humans. On 19 June 2006, we captured and attached a radio transmitter to the female after our 5th walk-in survey. We were unsuccessful in capturing the male after 9 attempts. We were not able to establish reproductive status by protocol, but are fairly certain that this pair did not nest in 2006 because we visited the female 19 times throughout the season and saw no young. She also exhibited no behavioral signs that would indicate nesting behavior. Throughout 2006 and 2007, we were able to record consistently good locations on this bird, as she typically did not venture far from the main drainage where her HRCA center appeared to be located. On 3 May 2007, we determined that she was nesting, but after several (6) subsequent visits, we concluded that her nesting attempt failed. We collected 92 pre-treatment locations, and 138 post-

treatment locations for this bird. On 30 August 30 2007, we recaptured her on our second walk-in survey and successfully removed her radio transmitter. This bird wore its transmitter for 437 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

ED121 Territory - Male

After ED121 Territory was randomly selected as a “replacement” site in late 2005, we visited the territory 4 times. We determined that the site contained a pair, but we were not able to establish reproductive status for the pair because they were quite uncooperative and shy of humans (see female history above). In 2006, we were unable to capture this male after 9 attempts.

ED124 Territory - Female

We conducted 7 walk-in surveys after we randomly selected this site in August 2005. Although we never detected a female, we knew that there was a female present in 2005 because we detected a juvenile at this site. On 25 May 2006, we captured a female and attached a radio transmitter to her during the third walk-in survey. We established non-nesting for this female during 2006, and were able to monitor her consistently through most 2006. She began to make wide-ranging movements in October, which made it difficult to follow her during that month. In early 2007, we could not locate her signal near her original area, but relocated her signal during an aerial search on 31 May approximately 12.5 km (7.8 miles) to the west of her original location. She was found with a new mate (see below) in this territory and we established non-nesting status by protocol in June. We collected 105 pre-treatment locations, and 66 post-treatment locations for this bird. On 12 September 2007, we removed her radio on our 1st walk-in survey. This bird wore its transmitter for 475 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

ED124 Territory - Male

We conducted 7 walk-in surveys after we randomly selected this site in August 2005. We found the male roosting with a juvenile, but we found no female present. We captured and attached a radio transmitter to the male on 1 June 2006 during our 7th walk-in survey. We were able to monitor this male consistently with 41 telemetry locations until he disappeared sometime after 10 August 2006. We failed to relocate him after conducting several extensive mobile searches by vehicle using an omni-directional antenna mounted on the vehicle as well as during an aerial search on 18 September 2006. We also conducted numerous night surveys in his presumed territory to attempt relocation in case his radio was not working, but he was still present. We continued to search for his transmitter signal during aerial search in May of 2007, but to no avail. His fate is unknown. This bird wore its transmitter for 70 days until his disappearance; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking judging by his behavior during walk-in surveys prior to his disappearance.

ED200 Territory - Female

We randomly selected this site late in 2005 as a “replacement” site. We surveyed this site 5 times in 2005, during which time we detected a male once. After 4 non-detection surveys at this site in early 2006, we detected a female on 20 June. We captured her and attached a radio transmitter on 21 June. Shortly after her capture, we encountered difficulties monitoring her because she began making wide-ranging movements and did not consistently stay in any area. We collected 39 pre-treatment telemetry locations during 2006, which were spread apart in both time and space, with most locations clustered at an area approximately 11 km (7 miles) from her original capture site. In 2007, she appeared to be more settled although she still showed considerable movement and we collected an additional 49 telemetry locations. Because of her wide-ranging movements (and the consequent lack in telemetry locations), we concluded that this bird was non-territorial (a “floater” sensu Franklin 1992) and dropped her from the analysis. We believe that including her in the analysis would have induced unknown confounding effects in the study. We detected her with a male one time over the length of the study on 7 June 2007. After 4 attempts, we captured and removed her radio transmitter on 18 September 2007. This bird wore its transmitter for 454 days; signal strength and quality was good most of the time we monitored her, but was seriously affected by topography at some locations. The bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

ED200 Territory - Male

We randomly selected this site late in 2005 as a “replacement” site. Thus, we were only able to survey this site 5 times, once during which we detected a single male. We detected no male at this site in 2006 despite 15 walk-in surveys (9 of which were walk-in surveys to observe the female ED200) conducted over the course of the field season. Thus, we concluded that there was no male because of 4 non-detection surveys and 9 visits to the single female during all of the 2006 field season.

Long Meadow Territory - Female

We surveyed the Long Meadow Territory 7 times during 2005, and detected a female during 2 of these surveys. This territory was part of the Eldorado regional study area (Seamans 2005). We established non-nesting status for this pair in 2005. This pair had been banded previously as part of our Eldorado demographic study so we knew the identities of these birds. Although we conducted 13 night surveys in 2006, we did not detect a female.

Long Meadow Territory - Male

We surveyed the Long Meadow Territory 7 times during 2005, and detected a male during 3 of these surveys. This territory was part of the Eldorado regional study area (Seamans 2005). We established non-nesting status with this pair in 2005. This pair had been banded previously as part of our Eldorado demographic study so we knew the identities of these birds. We conducted 13 night surveys in 2006 and only detected a male two times on 1 May and 1 June. Thus, we concluded that this site was unoccupied in 2006.

Rob's Peak Territory - Female

In 2005, we detected a female at Rob's Peak 8 times during 21 surveys and established non-nesting status with this bird. This territory was part of the Eldorado regional study area (Seamans 2005) and was paired with a male (see below). We believe that there was no female present at this site during 2006 or 2007. We conducted 31 walk-in surveys and 68 night-time telemetry surveys to observe the male (see Rob's Peak Territory male below) and never detected a female during these 2 years. Therefore, we concluded that there was no female in this territory available for capture and study.

Rob's Peak Territory - Male

During 2005, we detected a male 15 out of 21 surveys conducted at this site. We established non-nesting status of the female presumably paired with this male. This male would either not take or rarely take mice during a protocol survey. However, this pair was already banded, as it was part of the Eldorado regional study area (Seamans 2005). In 2006, we first detected this male on 27 April. We captured him on 20 June and attached the radio on our 7th capture attempt. We did not detect a female in either 2006 or in 2007 (see above). Thus, we believe that the male was single during these years. We were able to get consistent, valid telemetry locations with this bird for the length of the study. He did not normally roam far from his HRCA center. In 2007, we located him, on average, north-west of where he spent most of his time in 2006. We collected 95 pre-treatment locations, and 193 post-treatment locations for this bird. We failed to capture him during 14 visits to his territory in the fall of 2007. He did not show any interest in mice and he was extremely wary of the snare pole, and would fly away from his roost to a higher location as soon as the snare pole was extended, even when it was extended low to the ground. After the snow melted in 2008 we located his body on May 13th. This bird wore its transmitter for 693 days; signal strength was good throughout the time we monitored. We did not notice ill effects of the transmitter prior to his death. He died during the winter or spring, the cause of death was unknown.

Sugar Territory - Female

The Sugar Territory female was initially detected on 12 April 2005. This territory was part of the Eldorado regional study area so the birds were already banded (Seamans 2005). This female was paired (see below) and nesting in late April, but her nesting attempt had failed by early June. We visited this female 7 times in 2005. In 2006, we established non-nesting status by protocol; we then captured this female and outfitter her with a radio transmitter on our third visit of the season, 10 May 2006. We could not locate the female's radio signal after 27 June. We searched for her while walking in on the male and during several mobile vehicle searches of the area using an omni-directional antenna mounted on the vehicle. By 8 August, there was a new female seen with the original male. However, we did not attempt to capture her because we did not think there was sufficient time to collect valid pre-treatment location data (i.e., we found her 3 weeks before scheduled logging so realistically we would have had 15-20 valid locations). We searched for the transmitter signal of the original bird during an aerial survey on 18 September 2006 with negative results. We only had 6 locations for her by the end of 2006 when she was still missing. We again searched for her signal during an aerial survey on 31 May 2007 and located her signal emanating from near the town of

Greenwood, which was over 32 km (20 miles) from her original territory. After gaining permission to walk through the private land that we believed was her location, we recovered scattered remains of her body next to a building on 11 July, 2007. The cause of death was unknown. This bird wore its transmitter for 427 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

Sugar Territory - Male

We detected the Sugar Territory male on 13 April 2005. This territory was part of the Eldorado regional study area so the birds were color banded for identification (Seamans 2005). This male was paired and nesting with the female described above in late April, but had a failed nesting attempt by early June. We visited this male 7 times in 2005. In 2006, we established his non-nesting status by protocol; we then captured this male and outfitted him with a radio transmitter on our third visit of the season (same day as his mate), 10 May 2006. He lost his original mate shortly after 27 June and she was replaced by a new female that we first detected on 8 August 2006. Although we spent several hours each week with this bird, there were a few nights when we could not get accurate telemetry locations. He had a tendency to travel north and his signal would fade as he descended into deep canyons, making telemetry locations problematic at best. He remained consistently within his original area throughout the length of the study, and we recorded 95 pre-treatment locations and 246 post-treatment locations. He successfully fledged 2 young in 2007 and we removed his transmitter during our first recapture attempt on 21 August 2007. This bird wore its transmitter for 468 days; signal strength was good throughout the time we monitored and the bird showed no ill effects of radio marking (e.g., no obvious skin abrasions).

Whiskey Territory - Female

We visited the Whiskey Territory 15 times during 2005 and detected a female during 3 of these surveys. This female was paired, but we were not able to establish her nesting status. We did not detect any birds at this site in 2006 during 10 surveys.

Whiskey Territory - Male

We visited the Whiskey Territory 15 times during 2005 and detected a male on 6 survey occasions. This male was paired (see above), but we were not able to establish his nesting status. We did not detect any birds at this site in 2006 during 10 surveys.