

DISSERTATION

ECOLOGY OF THE CALIFORNIA SPOTTED OWL: BREEDING DISPERSAL AND
ASSOCIATIONS WITH FOREST STAND CHARACTERISTICS IN NORTHEASTERN CALIFORNIA

Submitted by

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In partial fulfillment of the requirements

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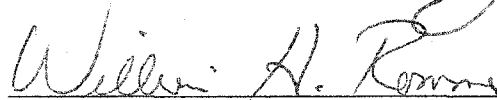
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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JENNIFER A. BLAKESLEY ENTITLED ECOLOGY OF THE CALIFORNIA SPOTTED OWL: BREEDING DISPERSAL AND ASSOCIATIONS WITH FOREST STAND CHARACTERISTICS IN NORTHEASTERN CALIFORNIA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

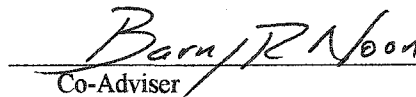
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ABSTRACT OF DISSERTATION

ECOLOGY OF THE CALIFORNIA SPOTTED OWL: BREEDING DISPERSAL AND ASSOCIATIONS WITH FOREST STAND CHARACTERISTICS IN NORTHEASTERN CALIFORNIA

The California spotted owl (*Strix occidentalis occidentalis*) inhabits coniferous and hardwood forest in California and selects stands dominated by large trees with moderate-high canopy cover for roosting and nesting. It is also found in areas dominated by medium-sized trees or low canopy cover. The owl has been at the center of political and administrative debates due to its association with commercially valuable forest. This study examined the demographic response of spotted owls to cover type composition within owl territories. Vegetation was mapped and classified within 2.4 km radius circles around 67 spotted owl sites in northeastern California. Vegetation polygons were classified by dominant tree size class, canopy cover, and density of remnant trees >76 cm diameter at breast height (dbh). I aggregated resulting classifications into cover types and used cover type composition within the different owl sites to explain variation in site occupancy, apparent survival probability and reproductive output, from 1993-1998, and nest success from 1990-2000. All analyses included data representing 2 spatial scales: core area (814 ha) and nest area (203 ha). Site occupancy was positively associated with the amount of the nest area dominated by large trees and high canopy cover within the nest area, and negatively associated with the amount of non-habitat and the amount of area dominated by medium-sized trees with high canopy cover. Furthermore, site occupancy decreased over time and with increasing elevation. Apparent survival probability varied annually and was positively related to the area of each cover type multiplied by the quotient proportion used / proportion available for each type, at both the nest and core scales. Reproductive output was negatively related to elevation and non-habitat within the nest area. Nest success was positively associated with the presence of large remnant trees within the nest stand. These findings reveal that although the California spotted owl is found in a variety of forest stand types, site occupancy, apparent survival and nesting success were all enhanced by increased amounts of forest cover types known

to be selected by the owl at the landscape scale. Reproductive output decreased with increasing amount of non-habitat.

Spotted owls are territorial, generally non-migratory, and strongly philopatric. Nevertheless, California spotted owls exhibited breeding dispersal during 7% of between-year observations of banded individuals ($n = 54$ of 743 occasions). Median breeding dispersal distance was 7 km (range = 1-33). Breeding dispersal probability was higher for paired owls which lost their mates, single owls, owls at lower quality sites, younger owls, and owls which failed to reproduce in the year preceding dispersal. To a lesser extent, dispersal probability was higher for males than females. I found no strong relationships between dispersal distance and any of the conditions that were associated with dispersal probability. Dispersal resulted in improved territory quality in 72% of cases. Single owls and those which lost their mates were usually paired following dispersal.

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INTRODUCTION

The spotted owl (*Strix occidentalis*) is a medium sized (500-800 g) nocturnal predator inhabiting forests and canyons of the western United States, northern Mexico, and southwestern Canada (Gutiérrez et al. 1995). Three subspecies are recognized: northern (*S. o. caurina*), California (*S. o. occidentalis*), and Mexican (*S. o. lucida*).

Administrative policy and political debate has centered on the California spotted owl due to its association with commercially valuable coniferous forest (USDA 1993, 1995, 1996, 1998a, 1998b, 2001a, 2001b, HFQLG 1998). The U.S. Forest Service, in its Sierra Nevada Forest Plan Amendment (USDA 2001a, 2001b), sought to balance the demand for timber production in the Sierra Nevada, with maintenance of habitat for spotted owls and forest carnivores, and the need to reduce the risk of catastrophic wildfire. Despite years of effort devoted to Plan preparation, the Forest Plan Amendment is currently being considered for revision and debate continues regarding the forest conditions required by California spotted owls for survival and reproduction.

Several studies (reviewed in Chapter 1) compared the forest cover types used by California spotted owls with cover types generally available, establishing the association between spotted owls and old and large tree components of forests at the landscape scale. I sought a deeper understanding of spotted owl habitat associations through modeling spotted owl demographic response variables (site occupancy, apparent survival and reproduction) as a function of cover types, conditioned on the owls already having selected territories within the landscape (Chapter 1). I used empirical data from a long term spotted owl demography study (Blakesley et al. 2001) in conjunction with vegetation maps and ground measurements taken in the immediate vicinity of spotted owls nests. The vegetation maps were supplied by Dr. JoAnn Fites of the U.S. Forest Service.

The second chapter of this dissertation addresses breeding dispersal in spotted owls, movements by territory holders between successive breeding seasons. Spotted owls are territorial, generally non-

migratory, and show very strong site fidelity. Nevertheless, some individual owls exhibit breeding dispersal. Condition-dependent dispersal assumes an owl assesses its fitness prospects in its current territory and chooses to search for improved conditions elsewhere (Ims and Hjermann 2001). I modeled the probability of breeding dispersal and breeding dispersal distance as a function of spotted owl sex, age, territory quality, previous reproduction, and pair status (Chapter 2). In addition, I evaluated the consequence of breeding dispersal by comparing pre- and post-dispersal territory quality. As in the first chapter, I used empirical data from a long term spotted owl demography study.

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Chapter 1

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

INTRODUCTION

The California spotted owl inhabits coniferous and hardwood forests of the southern Cascades, western Sierra Nevada, and central and southern coastal mountains of California (Verner et al. 1992). Its association with old and large tree components of forests at the landscape scale is well established. Throughout the Sierra Nevada, the owl selected forested stands dominated by large trees (>61 cm diameter at breast height [dbh]) and moderate-high canopy cover ($\geq 40\%$) for foraging (Call et al. 1992, Zabel et al. 1992), and nesting and roosting (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, LaHaye et al. 1997, Moen and Gutiérrez 1997). In addition, owls used forest stands dominated by intermediate sized trees (30 - 61 cm dbh) less than the availability of these stands in the landscape. At a finer spatial scale, stands used by owls for roosting contained trees > 100 cm dbh more frequently than randomly selected stands (Moen and Gutiérrez 1997).

The studies cited above were important in discriminating the cover types used by owls from cover types generally available across the forest landscape. All studies demonstrated that owls use the landscape in a non-random fashion. Deeper understanding of spotted owl ecology may be achieved by analyzing differences in spotted owl vital rates as a function of cover types *occupied by owls*, and other variables, including weather and prey availability. LaHaye et al. (1997) failed to find differences in reproductive success of spotted owls in southern California based on nest type, nest stand characteristics, or habitat type. Owl reproduction in the southern Sierra Nevada was correlated with several climate variables and positively correlated with foliage volume above the nest (North et al. 2000). In the same study area, owl reproductive output was positively correlated with forests having $\geq 50\%$ canopy cover and negatively

correlated with forests having <50% canopy cover within owl activity centers (Hunsaker et al. 2001). The study reported on here examines site occupancy, apparent survival and reproduction of California spotted owls in relation to forest stand characteristics in northeastern California.

Objectives

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

METHODS

DATA COLLECTION

Study area

The study area encompassed 2200 km² of the Lassen National Forest (LNF) and adjacent forested land in northeastern California (40°00'-40°50'N, 120°30'-121°40'W; Figure 1.1). One territory was in Lassen Volcanic National Park, and several territories included private land managed primarily for timber production. The majority of forested stands on the study area were classified as white fir-mixed conifer, and were composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and red fir (*Abies magnifica*). The study area was located at the southern end of the Cascade Geographic Province. However, it was included in the Sierra Nevada Province for Spotted Owl management purposes (e.g., USDA 2001a) and lay near the northern limit of the distribution of the California Spotted Owl. Elevations on the study area ranged from 1200-2100 m.

Timber harvest in the Sierra Nevada has primarily been accomplished through selective thinning. In contrast to the range of the northern spotted owl, clearcut areas are uncommon in Sierra Nevada coniferous forests, resulting in relatively continuous forest cover and few high contrast edges at the landscape scale (SNEP 1996).

Owl data

Data on owls were collected during an 11 year spotted owl demography study. Data collection followed a standardized field protocol similar to that used in studies of northern spotted owls (Franklin et al. 1996, Blakesley et al. 2001). Owls were located during night and daytime surveys and were captured, banded and resighted to estimate apparent survival probability. Occupancy data were recorded for each site in each year and categorized as 'pair', 'single' or 'unoccupied' after 6 complete 2.4 km radius surveys. Reproduction was determined for as many sites as possible based on standardized field procedures (Blakesley et al. 2001). Reproductive output was defined as the number of offspring fledged at a site in a given year (0, 1, 2+). This differs from the definition of fecundity, the number of female offspring fledged per female owl. Reproductive output was 0 for sites confirmed to be vacant or occupied by single male owls. Successful nests in 1993-1998 produced 1 or 2 fledglings with one exception of triplets in 1998. Subadult (1- and 2-year old) female spotted owls had lower reproductive rates than adult females (Blakesley et al. 2001) and exhibited higher rates of breeding dispersal (Chapter 2 of this Dissertation). The sample size of subadult owls was small; therefore, I excluded subadult owls from analyses. Not all territories were sampled every year ($n = 258$ records from 63 mapped sites, 1993-1998).

Vegetation mapping

Vegetation was mapped within 2.4 km radius circles centered on 67 spotted owl sites in and adjacent to the Almanor Ranger District of the Lassen National Forest. The area mapped comprised approximately the western 2/3 of the owl territories in the study area. Homogeneous vegetation polygons were delineated and characterized using color aerial photographs, two sets of digital orthophoto quads (1993 and 1998) and timber sale information (JoAnn Fites, U. S. Forest Service, pers. comm.) Separate maps were created for each year, 1993 -1998. The dominant tree size class, percent canopy cover and large tree density were estimated and assigned to 3-6 categories per variable for each polygon. The size class and canopy cover categories followed standards used by the USFS for timber mapping (e.g., Verner et al. 1992) because I wanted results to be compatible with Forest Service methods and policies and to be useful to their land use planning. Size class categories were: 0 (no trees), 1 (seedlings; <15cm diameter at breast height [dbh]), 2 (small trees; 15-29 cm dbh), 3 (medium trees; 30-61 cm dbh), 4 (large trees; >61

cm dbh), and 6 (multilayered). Canopy cover categories were 0 (<10%), S (sparse; 10-25%), P (poor; 25-40%), N (normal; 40-70%), and G (good; >70%). Large tree density (number of trees >76 cm dbh per ha) were: 0 (<1.2), 1 (1.2-4.9), 2 (4.9-14.8) and 3 (>14.8). A forest stand dominated by trees from 30-61 cm dbh with 50% canopy cover and 1 large tree per acre, for example, would be coded as 3N1.

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

Combinations of the 3 vegetation measures resulted in 36 different polygon classifications within the core areas ($\bar{x} = 17/\text{site}$, range = 9-26). To reduce the number of explanatory variables in modeling site occupancy, apparent survival probability and reproductive output, I created cover types by grouping polygon classifications based on current knowledge of spotted owl ecology (Table 1.1). SELECT consisted of cover types used by California spotted owls for nesting in greater proportion than available in the landscape (Verner et al. 1992). OTHER was composed of cover types used for nesting by spotted owls proportionately less than available in the landscape (Verner et al. 1992). I created additional categories of SELECT and OTHER as areas with canopy cover >70% (CCG), presence of remnant trees (REM) or both (CCGREM; see Table 1.1). HABSCORE weighted all of the cover types used for nesting by the quotient

proportion used / proportion available for each type (based on Verner et al.1992). The final cover type variable was NON, composed of non forest and forested stands not used by California spotted owls for nesting (dominated by small trees and/or low canopy cover; Verner et al. 1992).

I hypothesized that cover types selected by owls for nesting (SELECT, SELCCG, SELREM, SELCCGREM, and HABSCORE) would be positively associated with spotted owl reproductive output and apparent survival probability (Table 1.2). These competing variables may be considered alternate models of high quality spotted owl habitat, designed to elucidate which characteristics of forest stands (dominant tree size, canopy cover, presence of large remnant trees) were most related to spatial variation in spotted owl demographic rates. I expected NON to be negatively associated with spotted owl reproductive output and apparent survival probability.

I had no a priori basis for predicting the effects of cover types used by owls for nesting but not selected at the landscape scale (OTHER, OTHCCG, OTHREM or OTHCCGREM) on reproductive output nor apparent survival probability. However, I hypothesized that selected cover types with canopy cover > 70% and/or large remnant trees present (SELCCG, SELREM or SELCCGREM) may exhibit stronger positive relationships to owl life history traits when combined with non-selected cover types having canopy cover > 70% and/or large remnant trees present (SELCCG + OTHCCG, SELREM + OTHREM, or SELCCGREM + OTHCCGREM, respectively).

Nest stand measurements

Field personnel measured physiographic and vegetation characteristics immediately surrounding owl nest trees at 132 nests from 64 owl territories throughout the demography study area (Figure 1.1). Ten m wide sampling strip plots began 5 m from the nest tree and extended 30 m in each of the 4 cardinal directions. We measured dbh and height of all trees ≥ 40 cm dbh and snags ≥ 12 cm dbh, and all logs ≥ 25 cm diameter within the entire plots. We measured dbh and height of trees <40 cm dbh in the central third of each plot and estimated canopy cover 10 and 25 m from the nest tree using a spherical densiometer. In addition, we recorded nest tree species, nest type (top cavity, side cavity, platform), dbh and height of the nest tree, nest height, nest condition (live tree or snag), slope, aspect and elevation. I used the vegetation polygon layer in GIS to determine the cover type of stands containing owl nests.

DATA ANALYSIS

Site occupancy

I modeled site occupancy, O , as a function of forest cover types using logistic regression with an ordered multinomial response: no owls (0), single owl(1), owl pair(2), $n = 273$, using PROC LOGISTIC in SAS (SAS Institute 2000). I had noticed a declining trend in site occupancy over time on the study area. Therefore I modeled year as a linear trend (T) as well as categorical (t) and constant (no year effect). In addition to the a priori models (Table 1.2), I ran single cover type covariate models containing SELCCG, SELREM and SELCCGREM, and a set of post hoc models that added the variable NON to the original models. The above cover type models were run at 2 spatial scales (core and nest) in combinations with and without elevation, with and without T, with and without NON, yielding 214 models.

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

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

Apparent Survival

I used a subset of the owl capture history data from the demography study which contained records of nonjuvenile owls found at the 67 sites for which vegetation mapping was completed. For owls that moved between sites, I split capture histories so that each portion of the history was associated with its corresponding vegetation data ($n = 231$ capture histories from 203 individual owls at 67 sites). For owls that moved from one site to another, I did not record "loss on capture" at the initial site.

Consequently, estimated apparent survival probability, $\hat{\phi}$, was negatively biased. The purpose of this

analysis, however, was to determine which cover types were positively or negatively associated with persistence at a site and not to estimate apparent survival probabilities per se. By not recording loss on capture, when an owl dispersed from a given site it reflected negatively on the cover type composition of that site.

I used Tests 2 and 3 in program RELEASE (Burnham et al. 1987:77) to evaluate goodness of fit of the data set to open population mark-recapture models. I used maximum likelihood methods, based on an a priori set of product-multinomial models (Lebreton et al. 1992) to estimate apparent survival probabilities. I modeled the effects of vegetation covariates on apparent survival probabilities using a linear model framework with logit link functions. I used program MARK (White and Burnham 1999) to obtain maximum likelihood estimates and AICc for model selection.

I initially modeled time and sex effects without cover type covariates to determine the underlying structure of subsequent models. Only one set of cover type covariates may be included per individual capture history; i.e., I could not incorporate changes in habitat over time in this analysis. Therefore, I used mean amounts of cover types at a site as the vector of cover type covariates for all owls at that site. The candidate set of a priori models of apparent survival included time and sex effects and the forest cover types described above (Table 1.2).

I estimated variance components using program MARK (White and Burnham 1999) to measure how much process variance existed in the capture history data (Franklin et al. 2000). I ranked each owl site according to overall reproductive output, and then grouped the sites into 7 ranked categories ($n = 8-11$ sites/group, 63 sites total) and estimated apparent survival probability of each group. This was similar to looking at temporal variation, using "site quality" groups rather than year. The justification for these groupings was that a previous analysis indicated that fecundity and apparent survival probability were positively related on the Lassen study area (Blakesley, Appendix 1.A).

Reproduction

I modeled reproduction, R , as a function of forest cover types using binomial logistic regression (no juveniles produced [0], 1-3 juveniles produced [1], using PROC LOGISTIC in SAS (SAS Institute 2000). I used records for adult females only because subadult female spotted owls have much lower

fecundity than adult females (Blakesley et al. 2001). I used AICc for model selection and estimated \overline{R}^2 for the best model. I included year in all models because of the high annual variability in reproduction in this owl population (Blakesley et al. 2001). After running all a priori models with year and cover type covariates, I re-ran the models including elevation. In all cases, models with elevation had lower AICc than models without elevation. Therefore, I eliminated all models without elevation.

Nest success

A large sample of nest tree and nest stand measurements was available throughout the study area, with corresponding nest success data from 1990-2000 ($n = 174$ reproductive outcomes). Forest cover type data were available for the majority of these records ($n = 122$ reproductive outcomes; 89 successes, 33 failures). Although other analyses were restricted to 1993-1998 because of limited availability of annual vegetation maps, I included all years in this analysis because nest stands were rarely affected by timber harvest between 1990-1993 and 1998-2000 (personal observation). Nest stands that were harvested after the nest was used and before the area was mapped were eliminated from this data set ($n = 2$).

I used logistic regression with PROC LOGISTIC in SAS (SAS Institute 2000) to model nest success, S , as a function of nest tree and nest stand characteristics, cover type of the nest stand, and year, and used QAICc for model selection. I also created 3 variables for this analysis by breaking the cover type codes down into the variables: SizeClass, CoverClass, and Remnant (binary). I hypothesized that nest success would be affected by the interaction between dominant size class and remnant trees within the nest stand, with remnants being more important in size class 3 than size class 4 stands.

RESULTS

Territory composition

Seventy percent of the total mapped area, 78% of the owl core areas and 83% of nest areas were composed of forested stands dominated by trees ≥ 30 cm dbh (size class 3 or larger) with $\geq 40\%$ canopy cover (codes N and G; Table 1.3). The values of HABSCORE, SELECT, SELCCG, SELREM, SELCCGREM and OTHCCG (3G0, 3G1 and 3G2) all increased as the scale of analysis around site centers decreased. In contrast, the percent composition of OTHER decreased with decreasing area around site centers (despite OTHCCG being higher). The following cover types each comprised $<1\%$ of the total

mapped area and are grouped with similar cover types in summary statistics: 3P1, 3P2, 3P3, 4P0, 4P1, 4P2, 3N2, 3G2, 4G3, 6G1, 6G2.

The coefficient of variation (CV) was greater within nest areas than core areas for all cover types. There was generally more variation among sites in the original polygon classifications than in the aggregated cover types (Table 1.3). For example, within the nest area, CV for OTHER = 0.48 and CV for 3G0 (a component of OTHER) = 1.13 .

Several cover types were strongly correlated with each other (Appendix 1.B). Notably, $r = 0.90$ for SELECT and OTHER, $r = 0.88$ for HABSCORE and SELECT and $r = -0.62$ for HABSCORE and OTHER.

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

Of 92 unique nest trees representing 138 nesting events, only 4 trees, representing 5 nesting events were < 76 cm dbh, the size of remnant trees identified in air photo interpretation. However, 20 nest trees representing 30 nesting events occurred within stands classified as having < 1.2 remnant trees/ha (cover types 3N0 and 3G0). Therefore, many of the large nest trees occurred at densities $< 1.2/\text{ha}$ within their respective forest stands.

Timber harvest occurred within 18 nest areas and 37 core areas from 1993-1997. Within sites subject to timber harvest, total harvest ranged from < 1 -60% of nest areas ($\bar{x} = 10\%$) and < 1 -48% of core areas ($\bar{x} = 4\%$; Figure 1.3).

Site occupancy

All competitive models of site occupancy ($\Delta AICc < 5$) included a declining trend in occupancy over time; best model $\hat{\beta}(T) = -0.33$, $SE(\hat{\beta}) = 0.10$. Many models included ELEV as an explanatory variable (Table 1.4). When nest and core area models were considered together, the combined Akaike weight of core area models was $< 1\%$. Therefore, I presented results of nest area models only (Table 1.4). The best model (lowest AICc) was $\{O(T + SELCCG + OTHCCG + NON)\}$, with a positive coefficient for SELCCG and a negative coefficient for OTHCCG and NON; $\bar{R}^2 = 0.18$. This means that the amount of nest area dominated by large trees and canopy cover $> 70\%$ was positively associated with site occupancy whereas the amount of nest area dominated by medium-sized trees with canopy cover $> 70\%$ was negatively associated with site occupancy. The amount of nest area unforested or dominated by small trees was also negatively associated with site occupancy. Cumulative Akaike weights of all site occupancy models (Table 1.5) indicated that the time trend (T), NON, ELEV, SELCCG, and OTHCCG were important explanatory variables.

Apparent survival

Results of Tests 2 and 3 from program Release indicated that the capture history data fit the assumptions of open population mark-recapture models. The structure of the data before adding covariates included an effect of year on apparent survival probability and an effect of sex on recapture probability, model $\hat{\phi}(t)p(g)$. The best model was $\{\hat{\phi}(\text{Year} + \text{HABSCORE})\}$ within the nest area (Table 1.6). The second best model ($\Delta AICc = 0.47$) included HABSCORE within the core area. The third and fourth-best models ($\Delta AICc = 0.92, 0.93$) included SELREM within the core and nest areas, respectively. Coefficients for HABSCORE and SELREM were positive at both scales, meaning that apparent survival increased with increased amounts of cover types selected by the owls at the landscape scale, and increased amounts of stands dominated by large trees with normal to good canopy cover containing large remnant trees. Although the remaining models with one cover type covariate all explained more variation in apparent survival probability than the model $\{\hat{\phi}(t)p(g)\}$, (i.e. they had lower deviance than the base

model), the increase in number of parameters resulted in higher AICc values and therefore I did not consider the remaining models to be parsimonious.

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

Reproduction

The best model of reproductive output was {R (Year + Elev + NON) within the nest area} (Table 1.7), $\bar{R}^2 = 0.25$, $\hat{\beta}_{Elev} = -0.00078$, $SE(\hat{\beta})_{Elev} = 0.00035$, $\hat{\beta}_{NON} = -0.0080$, $SE(\hat{\beta})_{NON} = 0.0053$. The negative coefficients of Elevation and NON indicate that reproductive output was lower at higher elevation sites and lower with increasing amounts of the nest area dominated by small trees or unforested. The second-best model of reproductive output ($\Delta AICc = 0.26$) was 88% as likely as the best model, and had $\bar{R}^2 = 0.24$. Although many models with cover types other than NON explained some variation in reproduction ($\log(\mathcal{L})$ with cover type < $\log(\mathcal{L})$ without cover type), the models were not parsimonious.

Nest stand composition

Spotted owl nests were primarily cavities in very large live pines and firs (Table 1.8). Mean canopy cover in the immediate vicinity of the nest was >80% with little variation among nests. Nest tree dbh ranged from 38-219 cm; however, 90% of nest trees were ≥ 76 cm dbh. The number of hardwood stems was highly variable because very few sites contained a measurable hardwood understory. Among the continuous nest site variables measured, the only strong correlation (>0.50) was between the 2 canopy cover measures (Appendix 1.C).

Nest success

The best model of nest success was {S (Remnant + SizeClass)}, $\bar{R}^2 = 0.16$ (Table 1.9). The coefficients for Remnant was positive and the coefficient for SizeClass was negative, meaning that nest success was higher when large remnant trees were present in the nest stand, and higher in size class 3 than size class 4 stands.

DISCUSSION

Forest stand characteristics used for land management planning include size class of the dominant trees and total canopy cover. Strong relationships were found between tree size and canopy cover, and occurrence of spotted owls forest-wide (Gutiérrez et al. 1992). In contrast to landscape scale studies comparing used to available habitat, the analyses in this study were predicated on owls having selected a territory within the forested landscape. I sought to explain variation in site occupancy, apparent survival probability, reproductive output and nest failure based on differences in forest composition of spotted owl territory centers and nest tree measurements. The low variability in forest composition among nest and core areas of owl home ranges within the Lassen study area limited the explanatory power of forest composition. Some among site variation was lost when the original polygon classifications were aggregated into cover types. The strong correlations between cover types limited the information about spotted owl habitat provided by different cover types. Nevertheless, cover type did explain variability in the owl data and some trends emerged.

Relationships of cover type variables to demographic response variables were consistent as hypothesized, except for the variables OTHCCG, OTHREM and OTHCCGREM. The best model in analyses of site occupancy, apparent survival and nest success included positive relationships between the response variables and SELCCG, HABSCORE, or REMNANT. This indicates that although owls were found nesting and roosting in a variety of forest stand types, site occupancy, apparent survival, and nesting success all increased with increased amounts of forest cover types known to be selected by the owl at the landscape scale. Reproductive output decreased with increasing amount of non-habitat within the nest area.

The positive association between survival and fecundity in this study contrasts with the trade-off found for northern spotted owls in northwestern California, in which the amount of interior mature and old-growth forest was positively associated with survival and negatively associated with reproductive output (Franklin et al. 2000). Both survival and reproductive output were positively associated with the length of edge between mature/old-growth forest and other vegetation types, including younger forest (Franklin et al. 2000). In partial explanation of this pattern, Franklin et al. (2000) noted that dusky footed

woodrats (*Neotoma fuscipes*) are the primary prey of northern spotted owls in northwestern California (Ward et al. 1998) and are found in highest densities in sapling/brushy pole timber stands < 25 yr old (Sakai and Noon 1993).

Two important differences exist between conditions for the northern spotted owl in northwestern California and the California spotted owl in the Lassen study area. First, because clearcut timber harvest was relatively uncommon, structural differences between adjacent stands in the Lassen study area were often subtle. Second, the primary prey of California spotted owls in higher elevations of the Sierra Nevada and southern Cascades were northern flying squirrels (*Glaucomys sabrinus*; Verner et al. 1992). Flying squirrel densities in the Lassen study area were highest in old forest stands, lowest in shelterwood logged stands, and intermediate in young forest stands (Waters and Zabel 1995). Although the interspersed young and old forest stands appeared to benefit spotted owls where dusky footed woodrats dominated the owls' diet (Franklin et al. 2000), there is no a priori basis to expect young forest stands to benefit spotted owls where flying squirrels dominate the diet.

Nest area (203 ha) composition was a much better predictor of site occupancy than core area (814 ha), but relationships to apparent survival and reproductive output were similar for both spatial scales. Relationships between canopy cover and occupancy and reproduction of spotted owls in the southern Sierra Nevada were similar among 3 scales examined: 72, 203, and 430 ha (Hunsaker et al. 2001).

It is possible that a larger, more variable sample of owl sites would reveal stronger relationships between forest cover types and owl survival. Alternatively, site quality differences that affect owl fitness may also be related to vegetation characteristics that cannot be mapped with air photo interpretation such as ground cover conditions necessary to produce hypogeous fungi sporocarps, an important food for flying squirrels (Waters and Zabel 1995). Other technologies may provide remotely-sensed data to more precisely characterize forest cover used by spotted owls, e.g. LIDAR promises to provide data on vertical structure of the forest canopy. Some important habitat characteristics may occur at a much finer scale. Examples include conditions which enhance habitat for mammalian prey of the spotted owl, such as cavities in trees used by flying squirrels as dens.

In addition to vegetation variables in my models, year explained variation in site occupancy and survival, and elevation explained variation in site occupancy and reproduction. The negative time trend in site occupancy corroborates evidence from other analyses of Lassen spotted owl demographic data that the population declined during the study period (Blakesley et al. 2001, Franklin et al. 2002). Year was not an important variable in previous survival analyses from the Lassen study. Its appearance here may be an artifact of the smaller sample size (both owls and years) in this analysis than previous analyses.

Both survival and reproductive output declined with increasing elevation. Increased snowfall and colder temperatures at higher elevations on the Lassen study area could extract an energetic toll from the owls, decreasing survival and reproduction; spotted owl metabolic rate increases below 18°C (Weathers et al. 2001).

Other variables not included in this analysis which could directly affect spotted owl site occupancy, survival and reproduction include prey availability, predator density, competitor density, and disease. Great horned owls (*Bubo virginianus*) and northern goshawks (*accipiter gentilis*) prey upon spotted owls and occur in the Lassen study area. Field personnel on this study occasionally observed antagonistic encounters between goshawks and spotted owls, especially when fledgling owls were present. We also found remains of juvenile spotted owls that appeared to have been eaten by avian predators. The barred owl (*Strix varia*) expanded its range into California in 1981 (Dark et al. 1998). Barred x spotted owl hybrids first appeared in the Lassen study area in 1999 (unpublished data); as of 2001, 3 hybrid owls paired with spotted owls in historic spotted owl territories.

Methodological limitations

Several aspects of the methods used in this study may have limited my ability to draw stronger inferences from the data. First, the dominant size class and canopy cover of forest stands were lumped into broad categories, following those used by the Forest Service, because (1) the maps I used were built from maps used by the Lassen NF, and (2), I wanted results to be compatible with Forest Service methods and policies. However, Hunsaker et al. (2001) found a threshold of 50% canopy cover to be important to spotted owl reproduction. “Normal” canopy cover is defined as 40-70%, masking my ability to evaluate differences in response variables within this range of canopy cover. Also, stands dominated by all trees

>61 cm dbh were classified as size class 4. This is roughly half the mean size of trees used for nesting (117 cm dbh); a larger size class category may be more strongly associated with spotted owl site occupancy, survival or reproduction. Similarly, in 16 cases (within 3N0 & 3G0), remnant classification failed to account for the nest tree; I recommend mapping remnant trees at densities lower than 1.2 /ha in size class 3 stands.

To avoid fishing for results among thousands of possible models, I aggregated the individual cover types. This was another drawback to working with categorical data. The individual cover types had larger CV's than the aggregated cover types. Consequently, variation among sites lost in aggregation may have reduced my ability to explain variation in response variables.

Because spotted owls are long lived and have strong site fidelity (Chapter 2 of this Dissertation), I had insufficient data to separate the effects of territory quality and individual owl quality on reproduction and survival. Some of the observed variation in reproduction among territories may have been due to differences in owls' ability produce eggs or care for young. In magpies (*Pica pica*), individuals changed territories and/or mates between years frequently enough to compare the effects of territory quality and bird quality on breeding success (Goodburn 1991). Female quality accounted for 60% of the variance in magpie clutch size and male quality accounted for 70% of annual nesting success (Goodburn 1991).

Much more may be learned about spotted owl ecology through large scale manipulative experiments but results from such experiments will not be available for many years. In the meantime, spotted owl and other wildlife research would benefit tremendously if annual maps of forest cover were made available throughout the Sierra Nevada. These maps would be especially valuable if forest cover polygons contained continuous data on tree diameter distributions and canopy cover.

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Table 1.1. Cover types used for modeling site occupancy, probability of apparent survival and reproductive output of California spotted owls in Northeastern California.

Code	Definition	Cover types
SELECT	Large trees with Normal to Good canopy cover; multilayered.	4N0 4N1 4N2 4G0 4G1 4G2 4G3 6G1
SELCCG	Canopy Cover Good	4G0 4G1 4G2 4G3 6G1
SELREM	Remnant Trees present	4N1 4N2 4G1 4G2 4G3 6G1
SELCCGREM	Canopy Cover Good AND Remnant Trees present	4G1 4G2 4G3 6G1
OTHER	Large trees with poor canopy cover; medium trees with poor to good canopy cover; small trees with good canopy cover.	2G0 2G1 3P0 3P1 3P3 3N0 3N1 3N2 3G0 3G1 3G2 4P0 4P1 4P2
OTHCCG	Canopy Cover Good	2G0 2G1 3G0 3G1 3G2
OTHREM	Remnant Trees present	2G1 3P1 3P3 3N1 3N2 3G1 3G2 4P1 4P2
OTHCCGREM	Canopy Cover Good AND Remnant Trees present	2G1 3G1 3G2
HABSCORE	Medium and large cover types used for nesting, weighted by proportion used / proportion available.	$0.65*(2G) + 0.29*(3P) + 1.19*(3N+3G) + 0.48*(4P)$ $+ 2.26*(4N + 4G)$
NON	Nonforested and small trees.	All size 0 & 1; 2S 2P 2N 3S 4S

Table 1.2. Hypothesized relationships between covariates and site occupancy, apparent survival, and reproductive output of California spotted owls in northeastern California. Cover type acronyms are defined in Table 1.1

Models	Hypothesized relationship of covariates to site occupancy, apparent survival probability, and reproductive output
SELECT	Positive
SELECT + OTHER	Positive, unknown
SELECT + OTHCCG	Positive, positive
SELECT + OTHREM	Positive, positive
SELECT + OTHCCGREM	Positive, positive
SELCCG	Positive
SELCCG + OTHCCG	Positive, positive
SELREM	Positive
SELREM + OTHREM	Positive, positive
SELCCGREM	Positive
SELCCGREM + OTHCCGREM	Positive, positive
OTHER	Unknown
HABSCORE	Positive
NON	Negative
Year [Discrete]	Variable
Year (T) [Linear trend over time]	Negative for site occupancy
Elevation [Continuous]	Negative

Table 1.3. Cover type composition of total mapped area (1177 km²), core (814 ha) and nest area (203 ha) across 67 California spotted owl territories in northeastern California. Cover types are defined in Table 1.1. All means expressed as % area except HABSCORE.

Cover Type	Total Mapped Area		Core Area		Nest Area	
	Mean		Mean	CV	Mean	CV
SELECT	27		32	0.55	38	0.66
SELCCG	16		19	0.73	24	0.88
SELREM	22		26	0.70	31	0.83
SELCCGREM	13		17	0.85	21	1.03
OTHER	56		55	0.35	54	0.48
OTHCCG	19		25	0.56	29	0.80
OTHREM	15		16	0.92	16	1.19
OTHCCGREM	7		9	1.25	10	1.51
HABSCORE	117		129	0.19	142	0.21
NON	16		9	0.70	6	1.10
3P0	9		6	1.07	5	1.49
3P1, 3P2, 3P3	1		1	1.72	1	3.89
3N0	18		16	1.03	14	1.49
3N1, 3N2	6		5	1.28	4	2.35
3G0	12		15	0.78	18	1.13
3G1, 3G2	6		9	1.25	10	1.51
4P0, 4P1, 4P2	1		1	1.81	1	2.74
4N0	3		4	1.26	3	2.17
4N1	6		6	1.19	6	1.76
4N2	3		3	1.70	4	2.57
4G0	2		2	1.38	3	2.26
4G1	6		9	1.04	11	1.47
4G2, 4G3	7		8	1.54	10	1.75
6G1, 6G2	<1		<1	8.12	<1	8.12

Table 1.4. Models (95% Confidence set) of site occupancy (O) including cover type covariates for California spotted owls in northeastern California, 1993-1998 ($n = 273$). Models are ordered by AICc. Cover types are defined in Table 1.1. All models shown are for cover types within nest area; no core area models had $w_i > 0.004$.

Model	$\log(\mathcal{L})$	K	AICc	$\Delta AICc$	w_i
O (T + SELCCG + OTHCCG + NON)	-160.98	6	334.28	0.00	0.19
O (T + Elev + SELCCG + OTHCCG + NON)	-160.13	7	334.68	0.40	0.16
O (T + Elev + SELCCG REM + OTHCCG REM + NON)	-160.57	7	335.56	1.29	0.10
O (T + Elev + SELCCG REM + OTHCCG REM)	-161.74	6	335.79	1.52	0.09
O (T + SELCCG + OTHCCG)	-163.30	5	336.82	2.55	0.05
O (T + Elev + SELCCG + OTHCCG)	-162.44	6	337.19	2.91	0.05
O (T + SELCCG REM + OTHCCG REM + NON)	-162.44	6	337.20	2.93	0.04
O (T + Elev + SELCCG + NON)	-162.47	6	337.25	2.98	0.04
O (T + SELCCG REM + OTHCCG REM)	-163.60	5	337.42	3.14	0.04
O (T + Elev + SELCCG)	-164.26	5	338.75	4.47	0.02
O (T + SELECT + OTHCCG + NON)	-163.28	6	338.88	4.61	0.02
O (T + SELCCG + NON)	-164.43	5	339.08	4.80	0.02
O (T + Elev + SELECT + OTHCCG REM + NON)	-162.48	7	339.37	5.10	0.02
O (T + Elev + SELECT + OTHCCG + NON)	-162.58	7	339.58	5.30	0.01
O (T + Elev + SEL REM + OTH REM + NON)	-162.59	7	339.60	5.33	0.01
O (T + Elev + SELCCG REM + NON)	-163.79	6	339.89	5.61	0.01
O (T + Elev + SELECT + OTHCCG REM)	-164.08	6	340.48	6.20	0.01
O (T + SELCCG)	-166.17	4	340.48	6.21	0.01
O (T + Elev + SELCCG REM)	-165.24	5	340.70	6.42	0.01
O (T + Elev + SELECT + OTH REM + NON)	-163.19	7	340.81	6.53	0.01
O (T + Elev + SEL REM + OTH REM)	-164.31	6	340.93	6.66	0.01
O (T + SELECT + OTHCCG REM + NON)	-164.43	6	341.17	6.90	0.01
O (T + SELCCG REM + NON)	-165.51	5	341.24	6.96	0.01
O (T + Elev + SELECT + OTHER)	-164.57	6	341.46	7.18	0.01
O (T + SELECT + OTHCCG)	-165.88	5	341.98	7.70	0.00

Table 1.5. Cumulative Akaike weights (w_+) of covariates in models of Site Occupancy for California spotted owls in northeastern California, 1993-1998 ($n = 273$). Cover types are defined in Table 1.1. Covariates with $w_+ < 0.05$ are not shown.

Covariate	w_+	sign of $\hat{\beta}$
T (time trend)	0.99	Negative
NON	0.67	Negative
Elevation	0.58	Negative
SELCCG	0.55	Positive
OTHCCG	0.50	Negative
OTHCCGREM	0.32	Negative
SELCCGREM	0.31	Positive
SELECT	0.10	Positive

Table 1.6. Models of apparent survival probability (ϕ) including cover type covariates for California spotted owls in northeastern California, 1993-1999 ($n = 136$). All models included sex effects on probability of recapture ($K=2$). Models are ordered by AICc. Cover types are defined in Table 1.1.

Model	$\log(\mathcal{L})$	K	AICc	ΔAICc	w_i	Cover type $\hat{\beta}_i$ (95% CI)
ϕ (Year + HABSCORE nest)	-196.22	9	411.00	0.00	0.13	0.242 (-0.033 , 0.518)
ϕ (Year + HABSCORE core)	-196.46	9	411.48	0.48	0.10	0.228 (-0.053, 0.509)
ϕ (Year + SELREM nest)	-196.68	9	411.93	0.93	0.08	0.206 (-0.071, 0.483)
ϕ (Year + SELREM core)	-196.68	9	411.93	0.93	0.08	0.206 (-0.073, 0.486)
ϕ (Year)	-197.75	8	411.95	0.95	0.08	
ϕ (Year + SELCCGREM core)	-197.03	9	412.63	1.62	0.06	0.164 (-0.109, 0.438)
ϕ (Year + SELCCGREM nest)	-197.03	9	412.63	1.63	0.06	0.168 (-0.110, 0.446)
ϕ (Year + SELCCG core)	-197.06	9	412.69	1.69	0.06	0.159 (-0.111, 0.428)
ϕ (Year + SELECT core)	-197.07	9	412.71	1.71	0.06	0.162 (-0.112, 0.436)
ϕ (Year + SELECT nest)	-197.15	9	412.88	1.88	0.05	0.147 (-0.117, 0.411)
ϕ (Year + SELCCG nest)	-197.24	9	413.06	2.06	0.05	0.138 (-0.134, 0.410)
ϕ (Year + NON nest)	-197.29	9	413.15	2.15	0.05	-0.127 (-0.388, 0.133)
ϕ (Year + ELEV)	-197.31	9	413.18	2.18	0.04	-0.128 (-0.396, 0.140)
ϕ (Year + OTHER core)	-197.59	9	413.75	2.75	0.03	-0.078 (-0.350, 0.194)
ϕ (Year + OTHER nest)	-197.66	9	413.90	2.90	0.03	-0.055 (-0.321, 0.210)
ϕ (Year + NON core)	-197.67	9	413.91	2.91	0.03	-0.052 (-0.315, 0.211)

Table 1.7. Models (80% Confidence set) of annual reproductive output (R) of California spotted owls in northeastern California, 1993-1998 ($n = 258$). Models are ordered by AICc. Cover types are defined in Table 1.1.

Model	Area	$\log(\mathcal{L})$	K	AICc	ΔAICc	w_i
R (Year + Elev + NON)	Nest	-114.55	8	245.67	0.00	0.11
R (Year + Elev)		-115.74	7	245.93	0.26	0.09
R (Year + Elev + NESTING)	Nest	-115.27	8	247.13	1.46	0.05
R (Year + Elev + SELREM)	Nest	-115.39	8	247.37	1.70	0.05
R (Year + Elev + NESTING)	Core	-115.44	8	247.46	1.78	0.04
R (Year + Elev + SELECT)	Nest	-115.56	8	247.70	2.03	0.04
R (Year + Elev + SELREM + OTHREM)	Nest	-114.50	9	247.73	2.06	0.04
R (Year + Elev + NON)	Core	-115.63	8	247.84	2.17	0.04
R (Year + Elev + SELCCGREM)	Nest	-115.64	8	247.86	2.19	0.04
R (Year + Elev + OTHER)	Core	-115.67	8	247.92	2.25	0.03
R (Year + Elev + OTHER)	Nest	-115.72	8	248.02	2.35	0.03
R (Year + Elev + SELCCG)	Nest	-115.72	8	248.02	2.35	0.03
R (Year + Elev + SELREM)	Core	-115.73	8	248.04	2.37	0.03
R (Year + Elev + SELECT)	Core	-115.74	8	248.06	2.38	0.03
R (Year + Elev + SELCCG)	Core	-115.74	8	248.06	2.39	0.03
R (Year + Elev + SELCCGREM)	Core	-115.74	8	248.06	2.39	0.03
R (Year + Elev + SELECT + OTHREM)	Nest	-114.68	9	248.08	2.41	0.03
R (Year + Elev + SELREM + OTHREM)	Core	-114.85	9	248.42	2.75	0.03
R (Year + Elev + SELECT + OTHREM)	Core	-114.86	9	248.45	2.78	0.03

Table 1.8. Nest tree and nest stand structural variables around California spotted owl nest trees in northeastern California.

Code	Definition	Unique nests (<i>n</i> = 132)		Nest uses (<i>n</i> = 174) ^a	
		Mean	CV	Mean	CV
DBH	Nest tree diameter at breast height (cm)	117	0.29	118	0.28
Slope	Percent slope above and below nest tree	25	0.55	27	0.48
Elev	Nest tree elevation (m)	1714	0.09	1701	0.08
SmallCon	Number of conifer stems/ha 13-40 cm dbh	140	0.92	156	0.92
SmallHw	Number of hardwood stems/ha 13-40 cm dbh	13	3.51	16	3.18
Cancov10	Percent canopy cover 10 meters from nest tree	82	0.14	83	0.13
Cancov25	Percent canopy cover 25 meters from nest tree	81	0.16	81	0.16
LogVol	Log volume (m ³ /ha) of logs > 25 cm diameter	154	0.74	159	0.69
LiveBasal	Basal area/acre of trees > 40 cm dbh	54	0.38	53	0.38
SnagBasal	Basal area/acre of snags > 40 cm dbh	10	0.86	11	0.88
Summary					
TreeCond	Nest tree condition: live (L), snag (S)	L=97, S=35		L=134, S=40	
NestType	Nest type: platform: (P), top cavity (T), side cavity (S)	P=21, T=45, S=66		P=22, T=65, S=87	
Species	Nest tree species: fir (F), pine (P), other (O)	F=63, P=54, O=15		F=79, P=83, O=12	
Aspect	Aspect of slope at nest tree: N, E, S, W	N=45, E=35, S=22, W=30		N=59, E=35, S=31, W=49	

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

Table 1.9. Models of nest success including cover type, nest tree and nest stand structural covariates for California spotted owls in northeastern California, 1990-2000. Models are ordered by QAICc. Variables are defined in Table 1.8 and text. $n = 122$, $\hat{c} = 1.23$.

Model	$\log(\mathcal{L})$	K	QAICc	Δ QAICc	w_i
Remnant + SizeClass	-64.29	4	112.46	0.00	0.60
Remnant + SizeClass + Remnant* SizeClass	-64.26	5	114.58	2.12	0.21
Remnant	-67.49	3	115.50	3.04	0.07
CoverType	-63.23	7	122.00	4.55	0.06
TreeCond	-69.39	3	118.57	6.11	0.01
Elevation	-69.80	3	119.25	6.79	0.01
Intercept only	-71.22	2	119.43	6.97	0.00
SizeClass	-70.44	3	120.27	7.81	0.00
SnagBasal	-70.49	3	120.35	7.89	0.00
SmallHw	-70.59	3	120.52	8.06	0.00
CanCov10	-70.70	3	120.70	8.24	0.00
LogVol	-70.80	3	120.86	8.41	0.00
CoverClass	-71.01	3	121.20	8.74	0.00
SmallCon	-71.17	3	121.46	9.00	0.00
LiveBasal	-71.20	3	121.51	9.06	0.00
CanCov25	-71.21	3	121.52	9.06	0.00
DBH	-71.22	3	121.53	9.08	0.00
NestType	-70.81	4	123.01	10.55	0.00
Aspect	-69.93	5	123.76	11.30	0.00
Species	-70.77	5	125.12	12.66	0.00
Year	-67.39	12	136.00	23.55	0.00

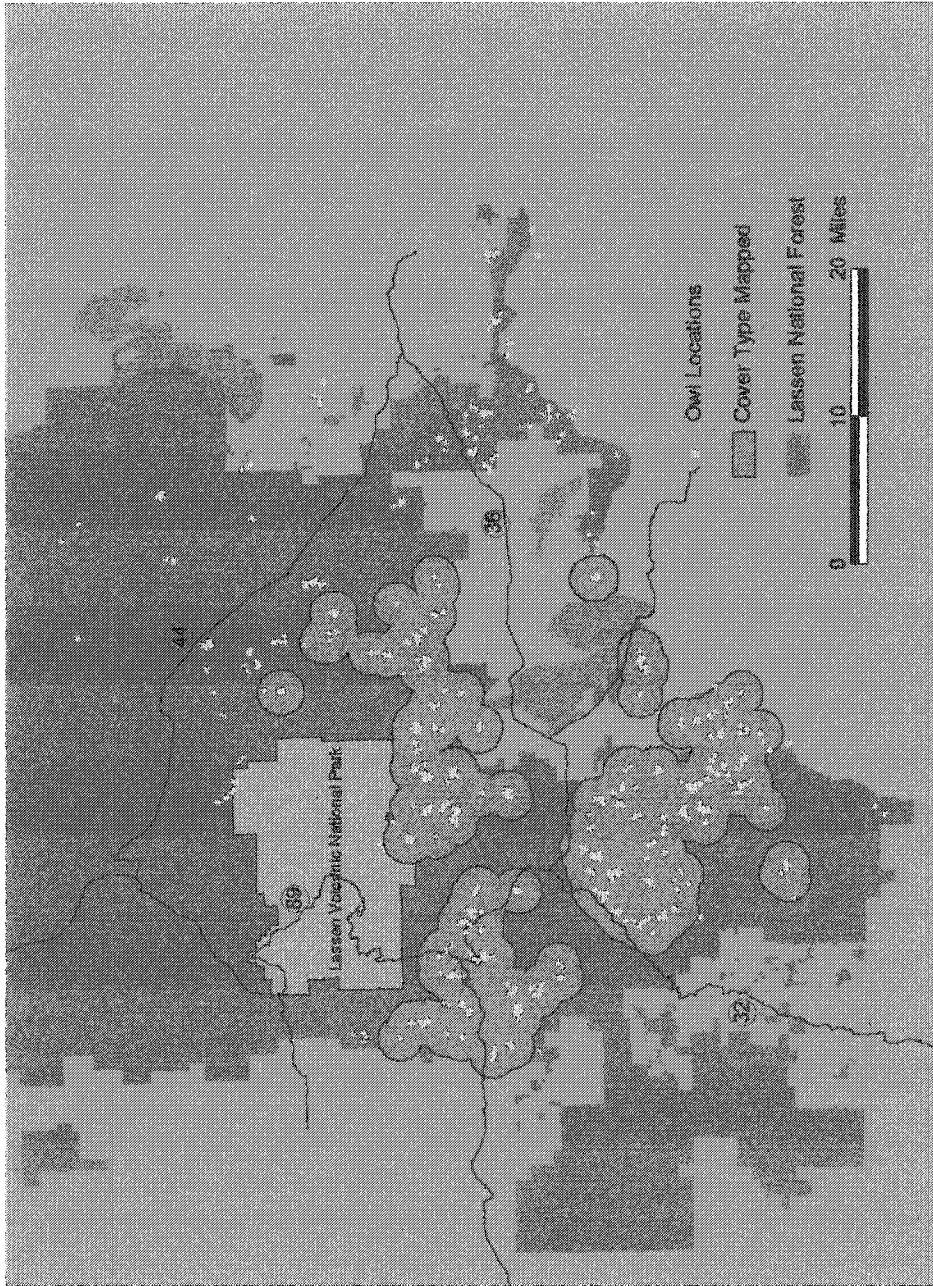


Figure 1.1 Locations of California spotted owls on the Lassen study area in northeastern California.

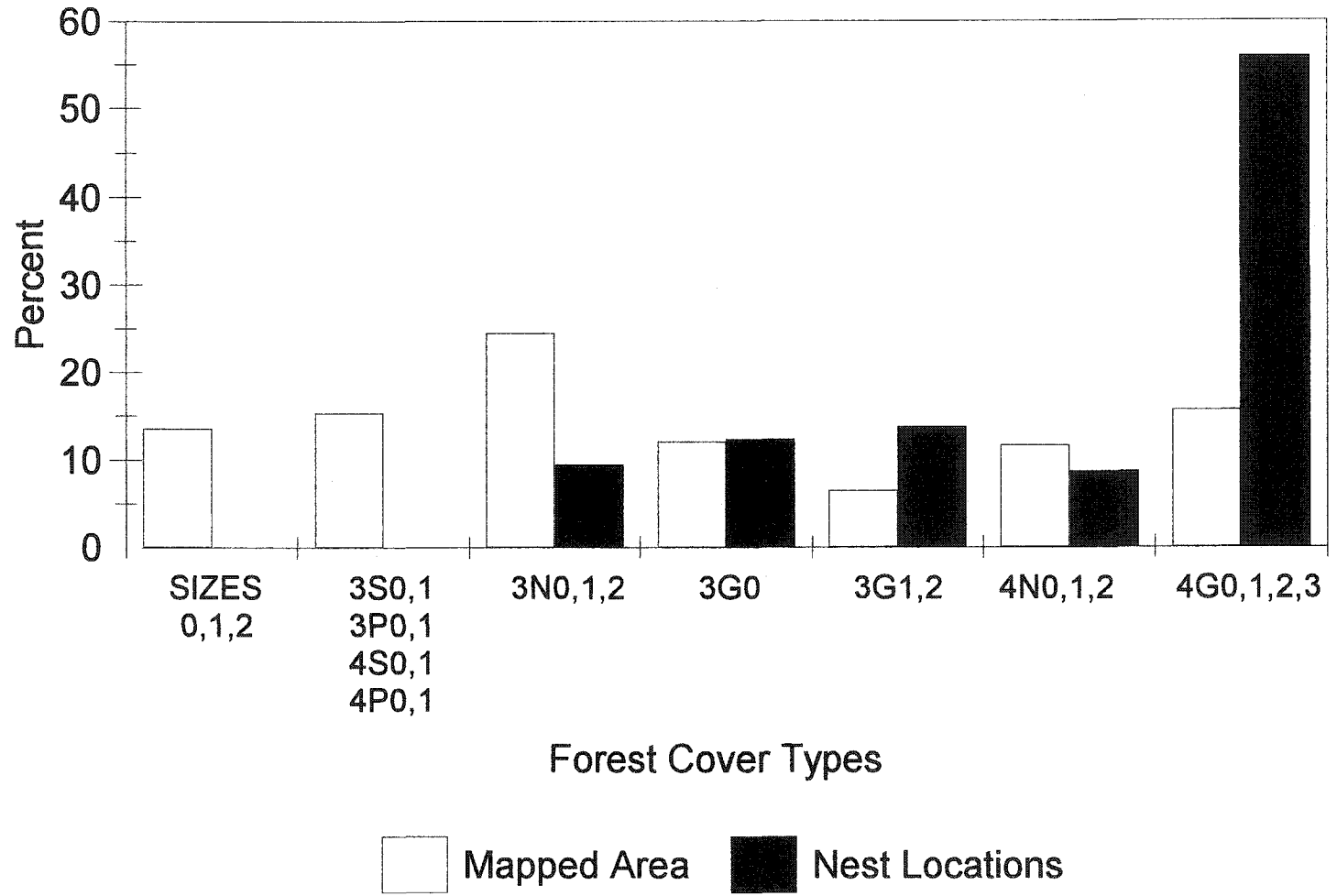


Figure 1.2. Cover type composition within 2.4 km radius of 67 California spotted owl site centers in northeastern California, and location of nesting events ($n=138$) within cover types. Cover type codes are described in text.

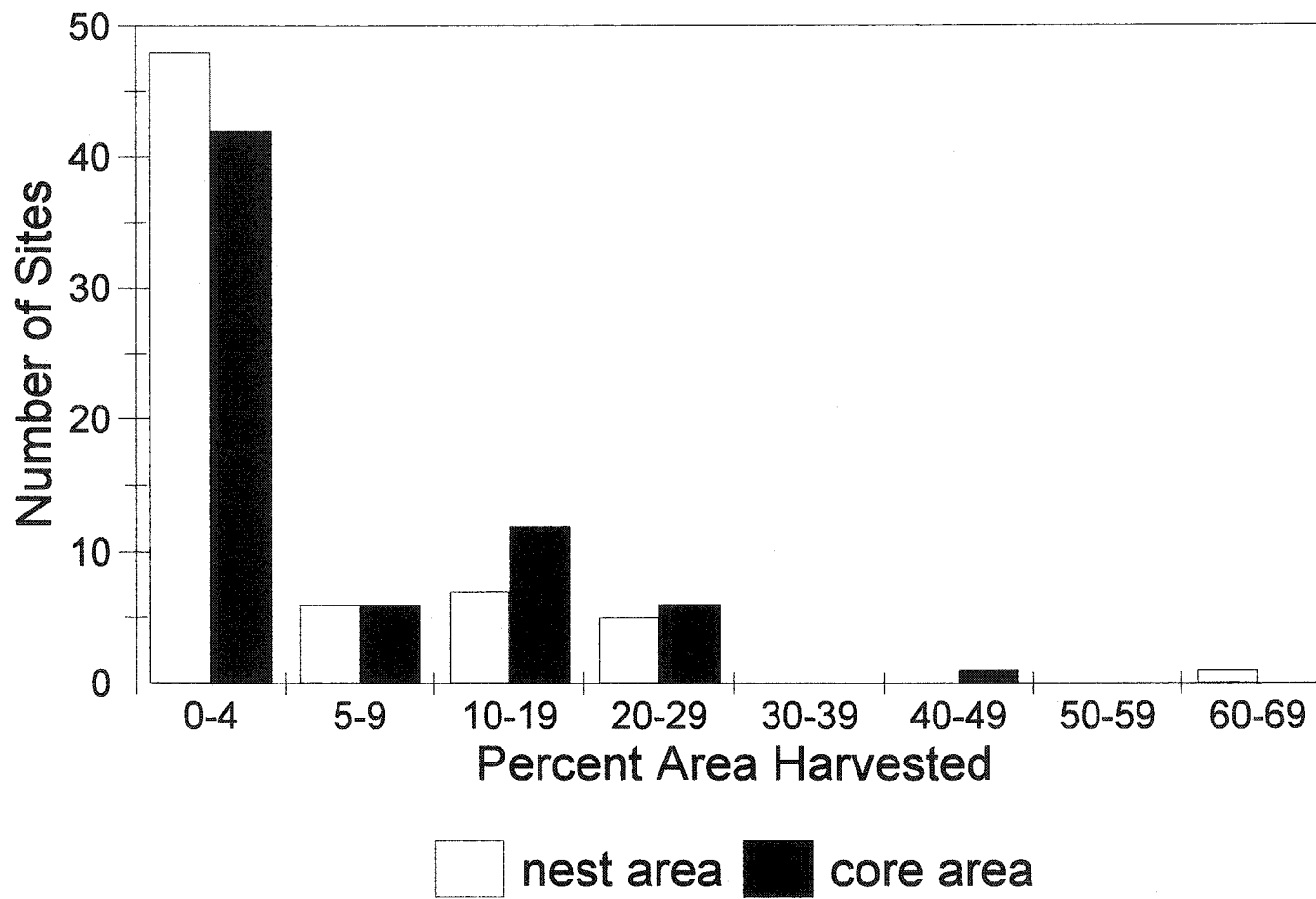


Figure 1.3. Timber harvest at 67 California spotted owl territories in northeastern California, 1993-1997.

Appendix 1.A. The positive association between apparent survival and reproduction within territories of California spotted owls in northeastern California, 1990-2001.

I calculated mean reproductive output of spotted owl territories, 1990-2001, following the methods for estimating territory quality, Q_i , in Chapter 2. I only included territories with ≥ 4 years of reproductive data. I then used Q_i as an individual covariate in estimating the probability of apparent survival, ϕ , 1990-2001, for owls occupying territories in which vegetation mapping was completed. For owls which moved between sites, I split capture histories so that each portion of the history was associated with its corresponding territory and used adult capture histories only ($n = 170$). I used program MARK (White and Burnham 1999) to obtain maximum likelihood estimates and AICc for model selection. I began by modeling effects of year and sex on ϕ and p (recapture probability) to determine the underlying structure of the data. The best model without covariates was $\{\hat{\phi}(\text{sex}), p(\cdot)\}$. Then I modeled ϕ with the addition of the covariate Q (mean reproductive output) both as $\{\phi(\text{sex} + Q), p(\cdot)\}$ and $\{\phi(\text{sex} * Q), p(\cdot)\}$. The result was that the 2 models with the reproduction covariate accounted for 99% of the Akaike weight. Because the additive model had 1 less parameter and $\Delta\text{AICc} = 0.08$, I report the results of the additive model, although inferences were similar from both models: $\hat{\beta}_Q = 0.417$, $SE(\hat{\beta}_Q) = 0.122$. This means that apparent survival probability is positively associated with mean reproductive output at owl territories.

Appendix 1B. Correlation coefficients among cover types within nest (203 ha) and core (814 ha) areas of 67 California spotted owl territories in northeastern California. Nest area data are above the diagonal; core area data are below the diagonal. Cover types are defined in Table 1.

Cover Type	SELECT	SELCCG	SELREM	SELCCGREM	OTHER	OTHCCG	OTHREM	OTHCCGREM	HABSCORE	NON
SELECT	1.00	0.79	0.93	0.77	-0.94	-0.53	-0.27	-0.22	0.91	-0.03
SELCCG	0.86	1.00	0.78	0.94	-0.73	-0.38	-0.25	-0.19	0.73	-0.04
SELREM	0.95	0.85	1.00	0.85	-0.87	-0.43	-0.15	-0.11	0.88	-0.04
SELCCGREM	0.85	0.97	0.89	1.00	-0.71	-0.32	-0.18	-0.13	0.76	-0.08
OTHER	-0.90	-0.77	-0.84	-0.74	1.00	0.52	0.26	0.19	-0.76	-0.24
OTHCCG	-0.28	-0.14	-0.23	-0.09	0.36	1.00	0.29	0.51	-0.41	-0.09
OTHREM	-0.10	-0.17	-0.03	-0.11	0.16	0.36	1.00	0.81	-0.22	-0.04
OTHCCGREM	-0.07	-0.07	0.00	-0.01	0.11	0.58	0.85	1.00	-0.18	0.00
HABSCORE	0.88	0.76	0.86	0.79	-0.62	-0.06	0.02	0.05	1.00	-0.29
NON	-0.03	-0.04	-0.02	-0.07	-0.30	-0.22	-0.14	-0.10	-0.36	1.00

(continued)

Appendix 1B, continued.

Cover Type	3P0	3P1,2,3	3N0	3N1,2	3G0	3G1,2	4P0,1,2	4N0	4N1	4N2	4G0	4G1	4G2,3	6G1
SELECT	-0.12	0.02	-0.48	-0.19	-0.40	-0.22	0.09	0.10	0.36	0.33	0.04	0.52	0.47	0.28
SELCCG	-0.01	-0.06	-0.41	-0.16	-0.27	-0.19	0.08	-0.19	-0.01	-0.03	0.14	0.59	0.61	0.25
SELREM	-0.24	-0.01	-0.47	-0.12	-0.39	-0.11	0.10	-0.15	0.39	0.32	-0.22	0.53	0.54	0.30
SELCCGREM	-0.19	-0.08	-0.40	-0.12	-0.24	-0.13	0.06	-0.16	0.00	0.00	-0.19	0.59	0.68	0.26
OTHER	0.13	0.02	0.53	0.21	0.42	0.18	-0.03	-0.12	-0.36	-0.32	-0.05	-0.49	-0.41	-0.25
OTHCCG	-0.17	-0.10	-0.27	-0.21	0.71	0.50	0.07	-0.09	-0.18	-0.24	-0.18	-0.34	-0.08	-0.15
OTHREM	-0.18	0.21	-0.21	0.53	-0.33	0.81	-0.02	-0.21	-0.02	0.03	-0.18	-0.25	0.00	-0.10
OTHCCGREM	-0.19	-0.02	-0.24	-0.01	-0.24	1.00	-0.03	-0.19	0.06	-0.07	-0.16	-0.24	0.06	-0.07
HABSCORE	-0.34	-0.07	-0.32	-0.12	-0.29	-0.18	0.10	0.10	0.30	0.30	-0.11	0.45	0.51	0.22
NON	0.06	-0.11	-0.19	-0.01	-0.11	0.01	-0.06	-0.04	-0.05	0.12	0.10	0.03	-0.12	-0.04
3P0	1.00	0.05	-0.01	-0.05	-0.07	-0.18	-0.11	-0.13	-0.06	-0.15	0.53	-0.05	-0.18	-0.08
3P123	-0.04	1.00	-0.10	0.04	-0.08	-0.02	0.07	0.03	-0.03	0.20	0.06	-0.14	0.02	-0.03
3N0	0.18	-0.07	1.00	0.03	-0.12	-0.24	-0.13	0.04	-0.17	-0.15	-0.02	-0.20	-0.31	-0.08
3N12	-0.06	0.39	-0.09	1.00	-0.22	-0.01	-0.11	-0.10	-0.12	0.08	-0.12	-0.06	-0.08	-0.05
3G0	-0.02	-0.05	0.00	-0.39	1.00	-0.24	0.09	0.07	-0.24	-0.21	-0.07	-0.18	-0.13	-0.11
3G12	-0.25	-0.04	-0.34	0.17	-0.32	1.00	-0.02	-0.20	0.06	-0.06	-0.16	-0.24	0.06	-0.07
4P012	-0.03	0.15	0.01	-0.10	0.13	-0.12	1.00	-0.12	0.12	-0.02	0.05	0.30	-0.18	-0.04
4N0	-0.12	0.14	-0.04	-0.07	0.07	-0.10	0.05	1.00	-0.12	0.09	-0.09	-0.10	-0.10	-0.06
4N1	-0.15	-0.10	-0.14	-0.06	-0.30	0.01	0.07	-0.16	1.00	-0.11	-0.05	0.14	-0.14	0.23
4N2	-0.18	0.14	-0.31	0.37	-0.26	0.03	-0.09	0.10	-0.14	1.00	-0.10	-0.08	0.07	-0.05
4G0	0.29	0.07	0.02	-0.14	0.00	-0.23	0.12	0.12	-0.12	-0.16	1.00	-0.03	-0.21	-0.05
4G1	-0.19	-0.09	-0.35	-0.18	-0.09	-0.17	0.09	-0.01	0.47	-0.08	0.09	1.00	-0.19	0.37
4G23	-0.25	-0.06	-0.39	-0.08	-0.02	0.12	-0.14	-0.15	-0.18	0.22	-0.26	-0.14	1.00	-0.07
6G1	-0.12	-0.07	-0.12	-0.03	-0.15	-0.05	-0.07	-0.08	0.55	0.00	-0.09	0.31	-0.08	1.00

Appendix 1.C. Correlation coefficients among nest tree and nest stand structural variables around 132 nest trees of California spotted owls in northeastern California. Variables are defined in Table 1.9.

Variable	DBH	Slope	Elev	SmallCon	SmallHw	Cancov10	Cancov25	LogVol	LiveBasal	SnagBasal
DBH	1.00	-0.08	0.02	0.08	0.02	-0.03	-0.04	0.01	-0.04	-0.03
Slope	-0.08	1.00	-0.25	0.04	0.11	0.16	0.18	-0.06	-0.24	0.08
Elev	0.02	-0.25	1.00	0.01	-0.24	-0.14	-0.17	-0.07	0.09	0.25
SmallCon	0.08	0.04	0.01	1.00	-0.10	0.02	0.10	0.35	0.08	-0.07
SmallHw	0.02	0.11	-0.24	-0.10	1.00	0.09	0.06	0.01	-0.08	0.01
Cancov10	-0.03	0.16	-0.14	0.02	0.09	1.00	0.63	-0.18	0.32	0.05
Cancov25	-0.04	0.18	-0.17	0.10	0.06	0.63	1.00	-0.12	0.42	-0.05
LogVol	0.01	-0.06	-0.07	0.35	0.01	-0.18	-0.12	1.00	-0.03	-0.03
LiveBasal	-0.04	-0.24	0.09	0.08	-0.08	0.32	0.42	-0.03	1.00	-0.01
SnagBasal	-0.03	0.08	0.25	-0.07	0.01	0.05	-0.05	-0.03	-0.01	1.00

Chapter 2

BREEDING DISPERSAL IN THE CALIFORNIA SPOTTED OWL

INTRODUCTION

Breeding dispersal in birds is commonly defined as territory or nest change between breeding attempts, and includes movements between successive nesting attempts within a breeding season (e.g., Jackson et al. 1989). For colonial nesting birds, dispersal can be between colonies or between individual nests within colonies; e.g., greater flamingos (*Phoenicopterus ruber roseus*) in the Mediterranean can disperse between nesting colonies in France and Spain, or within either of the colonies (Nager et al. 1996). For territorial birds, dispersal can be between disjunct populations or between territories within a population; e.g., red-winged blackbirds (*Agelaius phoeniceus*) can disperse between marshes or between territories within a marsh (Beletsky and Orians 1991).

California spotted owls (*Strix occidentalis occidentalis*) are territorial and in this study were distributed relatively evenly throughout the study area. Individual owls generally did not breed every year (Blakesley et al. 2001). Spotted owls rarely reneest within a breeding season, and if they do, it is within the same territory (Lewis and Wales 1993). Therefore, I used a more general definition of breeding dispersal herein: breeding dispersal is a territory change within a population between breeding seasons.

Both breeding and natal dispersal (the movement of young animals from their place of origin) in birds show a strong female bias regardless of whether measuring distance moved or proportion of birds moving (Greenwood 1980, Clarke et al. 1997). Greenwood (1980) hypothesized that female biased dispersal should occur in resource defense mating systems wherein males would benefit from remaining near their natal or breeding area and females would benefit from choosing among males (and the resources they defend) and avoiding inbreeding. In contrast, male biased dispersal tends to occur in species which defend mates rather than resources, and is found in most mammal species (Greenwood

1980). However, male biased dispersal was found by Clarke et al. (1997) in 22 of 102 avian species, which exhibited a variety of breeding system types, including mate defense.

If breeding dispersal is a non-random occurrence, it should result in increased fitness, including successful breeding, of dispersing individuals (“effective” dispersal of Greenwood and Harvey 1982). Béchichon et al. (1996) reviewed studies which estimated fitness components (survival and reproductive success) associated with dispersal for birds and mammals and found in 6 studies of birds that breeding dispersal resulted in increased survival in 1 of 10 cases, decreased survival in 1 case, and increased reproduction in 3 of 14 cases. Effects on survival and reproduction varied among sexes within species.

Adaptive hypotheses for breeding dispersal include inbreeding avoidance, mate choice, site choice, social constraints, and heritability (Payne and Payne 1993, Daniels and Walters 2000). Inbreeding avoidance is assumed to be a primary reason for natal dispersal (Greenwood 1980). With respect to breeding dispersal, inbreeding avoidance is important primarily in cooperatively breeding birds in which closely related individuals occupy the same territory (Daniels and Walters 2000). Mate choice and site choice imply that an individual disperses to obtain a better mate or nesting site, respectively, than it had previously. Reproductive failure may indicate a poor mate or poor site or both, and may often be a condition triggering breeding dispersal (e.g., Haas 1998). Mate and site choice are often confounded in monogamous species, especially for females (e.g., Warkentin et al. 1991). Predation avoidance hypotheses (e.g., Jackson et al. 1989) are a subset of site choice hypotheses. Korpimäki (1993) showed that breeding dispersal in Tengmalm’s owls (*Aegolius funereus*) increased with increased variability in prey density.

Social constraint hypotheses include the prediction that younger birds disperse at higher rates and greater distances than older birds, (Forsman et al. 2002) or that dispersal is dependent on population density (Newton and Wyllie 1992, Wiklund 1996). Finally, heritability assumes that dispersal behavior is genetically based (Payne and Payne 1993).

Before evaluating the preceding alternative hypotheses for any particular species, it is important to understand the constraints imposed by the species’ life history. The majority of spotted owls are non-migratory; consequently, territories are not vacated seasonally, which likely reduces the ability of a new

owl to displace the current territory holder. Both male and female spotted owls are territorial, strongly philopatric and generally pair for life (Gutiérrez et al. 1995). Nevertheless, some individuals undergo breeding dispersal and occasionally sever pair bonds (Forsman et al. 2002). Spotted owl populations can have high annual variability in reproduction, with 7 - 91% of pairs producing young in northeastern California in each year between 1990-1999 (Blakesley et al. 2001). In spotted owls and other long-lived species that breed infrequently, increased productivity post-dispersal may not be immediately apparent. The fitness consequences of dispersal are ideally determined by measuring lifetime reproductive success (Newton 1989). Territory change could fail to increase an owl's average annual fecundity, yet increase lifetime reproductive success by increasing the owl's survival probability. However, spotted owls can live > 16 yrs in the wild (Gutiérrez et al. 1995) making it difficult to obtain sufficient samples of lifetime reproductive success. As an alternative, site quality, measured as productivity of a territory over time, may indicate the potential of an owl to reproduce within a given territory (Forero et al. 1999).

External conditions influencing dispersal in spotted owls may include prey density, predator density, productivity and pair status (paired or single). Prey and predator density are difficult to measure across a population of spotted owls, and causes of nesting failure (e.g., predation) are rarely known. Clutch size in spotted owls is relatively invariable, with 1-2 eggs common and 3 eggs in a clutch rarer but synchronous across an owl population (Blakesley et al. 2001). Spotted owl age, sex, pair status and reproductive success, however, are routinely determined in spotted owl field studies and may be evaluated with respect to their relationship to breeding dispersal.

Breeding dispersal consists of 3 interdependent stages (Ims and Hjermann 2001). For spotted owls, these are: emigration from the original territory, transient movement, and immigration to the new territory. Dispersal movement was not directly observed in this study. I evaluated hypotheses corresponding to conditions prior to breeding dispersal and post-dispersal by spotted owls.

Objectives

The objectives of this study were (1) to identify factors associated with spotted owl breeding dispersal; (2) to determine whether these factors affect breeding dispersal distance; and (3) to evaluate the consequences of breeding dispersal.

METHODS

I made a priori hypotheses regarding the probability of breeding dispersal, dispersal distance and consequences of dispersal (Table 2.1). I predicted that dispersal probability would be higher for: (1) females than males, (2) younger owls than older owls, (3) single owls than paired owls, (4) owls that lost their mate (5) owls that failed to breed, especially females, and (6) owls in low quality territories. Furthermore, I expected that a higher quality site may override the tendency for owls that lost their mate or failed to breed to disperse. I predicted that dispersal distances would be farther for (1) females than males, (2) younger than older owls, and (3) owls from poorer quality territories. Finally, I predicted that, for dispersing individuals, (1) single owls that dispersed would be paired following dispersal, (2) widowed owls that dispersed would be paired following dispersal, and (3) post-dispersal territory quality would be higher than pre-dispersal territory quality.

DATA COLLECTION

Study Area

The Lassen study area encompassed 2200 km² of the Lassen National Forest and adjacent forested land in northeastern California (40°00'-40°50'N, 120°30'-121°40'W; Figure 1.1). One territory was in Lassen Volcanic National Park, and several territories included private land managed primarily for timber production. The majority of forested stands on the study area were mixed conifer, and were composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and red fir (*Abies magnifica*). The study area was located at the southern end of the Cascade Geographic Province. However, it was included in the Sierra Nevada Province for Spotted Owl management purposes (e.g., USDA 2001a, 2001b) and lay near the northern limit of the distribution of the California Spotted Owl. Elevations on the study area ranged from 1200-2100 m.

My colleagues and I studied California spotted owls (*S. o. occidentalis*) on the Lassen study area from April-August, 1990-2001, collecting data from individual color-banded owls annually: sex, age, territory location, social status and fledglings produced. Demographic parameters of the population and associations with forest stand characteristics were reported elsewhere (Blakesley et al. 2001, Blakesley

2003 [chapter 1 of this dissertation]). We followed a standardized field protocol to locate, capture, band and resight owls and to determine owl reproductive status (Blakesley et al. 2001). We determined owl sex based on the pitch of their calls. We identified owl age at the time of first capture as first year subadult ($1 < S1 < 2$ yr old), second year subadult ($2 < S2 < 3$ yr old), or adult ($A \geq 3$ yr old) based on plumage characteristics (Forsman 1981, Moen et al. 1991).

DATA ANALYSIS

For each interval between annual observations of an individual owl, I recorded whether or not the owl dispersed to a new territory and if the owl dispersed, I recorded the distance moved between territories. For each record, I added the following associated predictor variables: age class (S1, S2, A), juveniles produced (0=none, 1=1-3 fledged), social status (paired or single) and territory quality at the beginning of the interval, territory quality at the end of the interval, and mate loss during the interval. Mate loss was assumed during the interval if the mate was never again observed in the study. Because social status and mate loss were confounded, I combined these 2 binary variables into a single multinomial variable, Mate Loss (Y = paired & lost mate, N = paired & did not lose mate, S = single).

I used mean reproductive output of a territory (1990-2001) as the measure of territory quality, Q . Because data were missing for various territories each year and because population-wide reproduction had high annual variability (Blakesley et al. 2001), I estimated territory quality for territory i , Q_i , as follows:

$$Q_i = \left[\sum_j (x_{ij} - \bar{x}_j) \right] / n_i,$$

where x = no. juveniles produced, i = territory, j = year for which reproductive data were available for territory i , and n = number of years for which reproductive data were available.

Breeding Dispersal Probability

I modeled the probability of breeding dispersal, P_{BD} , as a function of sex, age class, reproduction, mate, and territory quality with logistic regression using PROC LOGISTIC in program SAS (SAS Institute 2000). I also modeled the interactions between territory quality and age class, and territory quality and mate, and sex and reproduction. In addition to the global model, I ran all possible subsets of

the predictor variables to discover whether or not a reduced-parameter model would be more parsimonious.

I used Akaike's Information Criterion corrected for small sample size (AICc) for model selection after checking for overdispersion in the data; overdispersion is indicated when deviance/degrees of freedom of the global model > 1 . Akaike weights, w_i , estimate the relative predictive strength of each model and may be viewed as the weight of evidence for model i (Burnham and Anderson 2002:75-77). Evidence ratios, w_i/w_k , express the relative likelihood of model i vs model k (Anderson and Burnham 2002). Because the same variable may appear in several competing models, I estimated the relative importance of each variable by calculating the cumulative Akaike weights, $w_+(j)$, where $w_+(j)$ is the sum of w_i across all models in the set in which variable j occurred (Burnham and Anderson 2002:77-79).

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

Dispersal Distance

I modeled breeding dispersal distance as a function of age class, mate, sex, pre-dispersal territory quality and post-dispersal territory quality. I modeled dispersal distance with general linear models using PROC GENMOD in program SAS (SAS Institute 2000) and used AICc for model selection. I linearized dispersal distance data with a logarithmic transformation. I estimated lognormal probability density functions for adult females, adult males, subadult females, and subadult males using the Solver function in Excel (Liengme 2002).

Consequences of Breeding Dispersal

I compared the quality of each owl's pre-dispersal territory with its post-dispersal territory. I also determined the post-dispersal pair status of single owls that dispersed.

RESULTS

Of 279 banded non-juvenile owls on the study area from 1990-2001, 203 were seen in ≥ 2 years, yielding 946 owl/year observations. Breeding dispersal occurred in 54 of the resulting 743 intervals (7% of potential occasions), including 4 cases of pair bond separation (divorce). In each case of divorce, the

female owl moved to a new territory and the male remained on the old territory. In 23 cases, owls dispersed to adjacent territories, including the only 2 cases in which owl pairs dispersed together. First year subadults (S1) exhibited the highest dispersal probability (45%), followed by second year subadults (24%) and adults (5%; Figure 2.1). In 32 cases, owls were missing for 1 or more years before being resighted (12 philopatric, 20 dispersers). Sufficient data were available to model dispersal probability for 27 dispersal events and 508 cases of territory fidelity.

Breeding Dispersal Probability

The best model of breeding dispersal probability included age class, reproduction, mate, territory quality, and interactions between reproduction and territory quality and mate and territory quality, $\bar{R}^2 = 0.40$ (Table 2.2). Parameter estimates of the best model (Table 2.3) indicated probability of dispersal increased for first year subadults, and to a lesser extent for second year subadults, increased for single owls and decreased for paired owls that did not lose their mates. Although territory quality and reproduction each had $SE(\hat{\beta}) > \hat{\beta}$, the interaction between these variables had a strong influence on dispersal probability; $SE(\hat{\beta}) \approx 0.5 * \hat{\beta}$. The interaction term (Reproduction*Quality) effect indicates owls that did not reproduce were less likely to disperse with increasing territory quality. The estimate for age class S2 also had $SE(\hat{\beta}) > \hat{\beta}$ but the estimate for S1 had $SE(\hat{\beta}) \approx 0.5 * \hat{\beta}$. This may be explained by the smaller difference in breeding dispersal probability between second year subadults and adults than between first year subadults and adults (Figure 2.1).

The global model (including all variables and interaction terms) was the second-best model, and was closely competing with the top model ($\Delta AICc = 0.25$), with $\bar{R}^2 = 0.42$. The interaction between sex and reproduction indicated that females that did not reproduce were more likely to disperse than males that did not reproduce ($\hat{\beta} = 0.553$, $SE(\hat{\beta}) = 0.334$). The sex effect alone was insignificant ($\hat{\beta} = -0.081$, $SE(\hat{\beta}) = 0.333$). The third-best model was also closely competing ($\Delta AICc = 0.85$) and consisted of

fewer parameters: age class, mate, site quality and the interaction between mate and territory quality.

Cumulative Akaike weights (Table 2.4) confirmed strong support for mate, territory quality, age class, and less strongly, reproduction and the interaction between mate and territory quality.

Dispersal Distance

Median dispersal distance for adult females, adult males, subadult females and subadult males were 9, 8, 4, and 10 km, respectively (Figure 2.2). Median dispersal distance for all owls combined was 7 km (range = 1-33). Estimated probability density functions had slightly different shapes among sex and age classes (Figure 2.3). Adult females had the flattest distribution, reflecting a higher probability of moving greater distances than the other sex/age classes. In contrast, adult males had the most peaked distribution, with the majority of adult males dispersing < 5 km. The best model of dispersal distance was {D(Pre-dispersal territory quality)}, $\hat{\beta}=0.991$, $SE(\hat{\beta})=0.535$, adjusted $R^2 = 0.10$ (Table 2.5). The intercept only model, however, was closely competitive ($\Delta AICc = 1.05$), evidence that pre-dispersal territory quality was somewhat weak in predicting dispersal distance. All of the remaining models had $\Delta AICc >$ the intercept only model; I did not consider them to be informative. Breeding dispersal distances were distributed evenly relative to each of the independent variables (Figure 2.4).

Consequences of Breeding Dispersal

Territory quality data were available for 39 of the owls that dispersed. Owls that dispersed tended to upgrade their territory quality, with 72% of dispersal movements to a territory of higher quality than the original territory (Figure 2.5).

Of the owls that dispersed, 4 females and 4 males were single prior to dispersing. All 4 females and 3 males were paired following dispersal. Of widowed owls, 13 of 16 were paired following dispersal; pair status of the remaining 3 owls was not determined following dispersal.

DISCUSSION

Breeding Dispersal Probability

California spotted owls exhibited breeding dispersal at average annual rates similar to northern spotted owls: first year subadults 32%, second year subadults 20%, adults 8%, overall 8% ($n > 5000$;

Forsman et al. 2002; data adjusted to the calculations used herein). These relatively low rates of dispersal for adult spotted owls may reflect a high cost of breeding dispersal relative to the benefits of philopatry. Animals that disperse must compete with conspecifics for vacant territories, search for resources in unfamiliar areas, and possibly traverse suboptimal habitat with increased risk of starvation and/or predation. Philopatry, on the other hand, is presumed to provide more efficient exploitation of food resources and refugia from predators, and competitive advantage in territorial disputes (Greenwood and Harvey 1982). Breeding dispersal rates among other raptor species were highly variable. In a 16 year study of Cooper's hawks (*Accipiter cooperii*) in Wisconsin, 0 males and 15% of females dispersed ($n = 98$ and 71 respectively; Rosenfield and Bielefeldt 1996). Breeding dispersal rates for nonmigratory barn owls (*Tyto alba*) in Utah were approx. 4% annually ($n > 500$; Marti 1999). In 3 populations of sparrowhawks (*Accipiter nisus*) in Scotland and England with different population trends, approximately 30% of birds dispersed annually ($n = 799$; Newton and Wyllie 1992). Among migratory black kites (*Milvus migrans*) in Spain, 26% of males and 33% of females changed territories annually ($n = 121$ and 122, respectively; Forero et al. 1999). Similarly, among migratory lesser kestrels (*Falco naumanni*) in Spain, 19% of males and 34% of females dispersed annually ($n = 173$ and 313, respectively; Serrano et al. 2001). Thirty nine percent of male and 72% of female merlins (*Falco columbarius*) in Saskatchewan dispersed in a mostly non-migratory population ($n = 28$ and 39, respectively; Warkentin et al. 1991).

My a priori hypotheses were supported except that the effect of sex on dispersal probability was marginal. Younger age classes, mate loss, unpaired status and low territory quality were the strongest predictors of breeding dispersal. Failure to produce young had a moderate influence on dispersal probability. Studies of other raptors revealed similar relationships. In non-migratory populations of sparrowhawks, breeding failure was followed by increased dispersal of females (Newton and Wyllie 1992, Newton 2001). Nest predation increased breeding dispersal in merlins (Wiklund 1996). Among black kites, the probability of breeding dispersal was higher from low-quality sites and following both breeding failure and mate loss (Forero et al. 1999). Both sexes showed an increasing tendency to stay on a territory with age in northern spotted owls (Forsman et al. 2002), sparrowhawks (Newton and Wyllie 1992, Newton 2001) and black kites (Forero et al. 1999). In lesser kestrels, the decreasing probability to

disperse with age was explained by decreasing probability of leaving a colony with increasing breeding experience in the colony (Serrano et al. 2001).

I found a negligible sex effect in breeding dispersal probability by California spotted owls even though female biased dispersal was found in the northern spotted owl (Forsman et al. 2002). This may be due in part to my smaller sample compared to that of Forsman et al. ($n = 440$; 2002). Additional studies showed female biased dispersal in black kites (Forero et al. 1999), merlins (Warkentin et al. 1991, Wiklund 1996), lesser kestrels (Serrano et al. 2001), Cooper's hawks (Rosenfield and Bielefeldt 1996) and northern goshawks (*Accipiter gentilis*; Detrich and Woodbridge 1994). However, the only raptor showing male biased dispersal probability among 7 species reviewed by Clarke et al. (1997) was the goshawk.

Divorce rates in California spotted owls were low and females moved in all observed cases of divorce. The sex bias may indicate that male spotted owls have stronger site fidelity than female spotted owls, however, the sample size was quite small. Many of the studies reviewed by Clarke et al. (1997) reported that sex biases were only found with "widowed" or "divorced" individuals.

Dispersal Distance

My hypotheses regarding dispersal distance were not supported; subadult and single owls did not move farther than other owls. In contrast younger northern spotted owls moved farther than older owls (Forsman et al. 2002). In merlins, females moved farther than males, and male breeding dispersal distance decreased with increasing population density (Wiklund 1996). In this study, 43% of dispersal events (92% of dispersals < 6 km) were to adjacent territories. Home ranges of spotted owl pairs overlap (Forsman et al. 1984, Zabel et al. 1992), providing the opportunity for owls to easily discern vacancies in adjacent territories. For owls not moving into adjacent territories, it is unknown how far or by what route the owls actually traveled before finding a territory vacancy (Wiens 2001).

A dispersing owl's new territory was often already occupied by an owl of the opposite sex that was present the previous year. There was no evidence that owls displaced territory holders; e.g., when a male owl from territory a in year i was found in territory b in year $i+1$, we did not also find the male from territory b in year i at territory c in year $i+1$. Barred owls (*Strix varia*) expanded their range into

California from the north in 1981 (Dark et al. 1998). Only 1 barred owl was detected through 2001 on the Lassen study area, although several spotted \times barred owl hybrids were observed holding territories and paired with spotted owls, beginning in 1999 (unpublished data). The range expansion of barred owls in Oregon and Washington appeared to displace spotted owls when barred owls were detected within 0.8 km of spotted owl territory centers (Kelly et al. 2003). Future study may reveal whether spotted owls are displaced by barred owls on the Lassen study area, and if so, whether displaced spotted owls are a random subset of territorial owls.

Breeding dispersal distance estimates would be biased towards shorter distances if owls moved beyond the study area boundary (Koenig et al. 1996). This bias was probably very small for the following reasons. Breeding dispersal distances for only 2 owls were > 23 km whereas 50% of observed natal dispersal distances among the same territories were > 23 km (range 3-76 km, $n = 36$; unpublished data). Owls undergoing natal and breeding dispersal had equal probability of being detected as residents on their new territories within the study area. Therefore, it is unlikely that dispersing non-juvenile owls moved farther than recorded and remained undetected. Furthermore, median breeding dispersal distance for northern spotted owls within and between contiguous study areas in Oregon and Washington was 3.5 km ($n = 440$; Forsman et al. 2002). Natal dispersal distances were also greater than breeding dispersal distances for 61 of 69 terrestrial bird species reviewed (Paradis et al. 1998).

The timing and duration of dispersal in spotted owls is unknown. Very few philopatric owls went unobserved when presumably they were present in their territories ($< 2\%$ of intervals between observations were > 1 yr). In contrast, 36% of dispersing owls were not seen for ≥ 1 yr. This time lag may reflect that, for some owls, the dispersal process may take > 1 year. Some owls may enter a floater (non-territorial) population before finding a vacancy in a suitable territory. While non-breeding as a floater may be a cost of breeding dispersal (Danchin and Cam 2002), this cost may be offset by increasing the probability of obtaining a higher quality territory in the future. Although floater owls are seldom detected, owls banded as juveniles provide further evidence that non-territorial spotted owls exist: the majority of banded juvenile owls detected on the Lassen study area as territory holders were first reobserved 2 or more years after their natal year (unpublished data). Resident floaters within a population

of great horned owls (*Bubo virginianus*) occupied home ranges roughly 5 times the size of regular territories, with concentrated use at the peripheries of the territories (Rohner 1997).

Consequences of Breeding Dispersal

Post-dispersal territory quality was higher than pre-dispersal territory quality for most owls, as hypothesized. Although I was unable to directly measure fitness pre- and post-dispersal, owls that moved to higher quality territories increased their potential for reproducing. Some owls, however, moved to sites of lower quality, as defined by mean reproductive output. This may reflect owls dispersing for reasons other than site quality, e.g., they may be single owls dispersing in search of a mate, which would necessarily increase their probability of reproducing, even in a poor quality territory. Alternatively, owls dispersing to lower quality territories may have been responding to predators or some other factor I did not measure.

Breeding dispersal in northern (Forsman et al. 2002) and California spotted owls (this study) was infrequent and condition-dependent (Ims and Hjermann 2001). Any future increase in rates of breeding dispersal for these populations may indicate a decline in territory quality, decreased nesting success, increased adult mortality, or increased competition with barred owls.

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Table 2.1. A priori predictions for factors affecting breeding dispersal probability, dispersal distance, and consequence of dispersal in California spotted owls in northeastern California. Selected supporting references are in parentheses.

Factor	Prediction		
	Dispersal Probability	Dispersal Distance	Dispersal Consequence
Sex	Females are more likely to disperse than males. (Greenwood 1980, Warkentin et al. 1991, Rosenfield and Bielefeldt 1996, Wiklund 1996, Clarke et al. 1997, Forero et al. 1999, Serrano et al. 2001, Forsman et al. 2002)	Females disperse farther than males. (Greenwood 1980, Wiklund 1996, Clarke et al. 1997)	
Age	Younger birds are more likely to disperse than older birds. (Newton and Wyllie 1992, Forero et al. 1999, Serrano et al. 2001, Forsman et al. 2002)	Dispersal distance decreases with increasing age. (Forero et al. 1999, Forsman et al. 2002)	
Social status	Single birds are more likely to disperse than paired birds. (Forsman et al. 2002)		Single birds are paired following dispersal. (Payne and Payne 1993)
Mate loss	Birds that lose their mate are more likely to disperse than those that retain their mate. (Forero et al. 1999, Forsman et al. 2002)		Widowed birds are paired following dispersal.
Reproduction	Birds are more likely to disperse following reproductive failure than success. (Newton and Wyllie 1992, Payne and Payne 1993, Wiklund 1996, Forero et al. 1999)		
Territory quality	Birds are increasingly likely to disperse with decreasing territory quality. (Forero et al. 1999)	Birds dispersing from poorer quality territories move farther (Forero et al. 1999)	Territory quality improves following dispersal. (Forero et al. 1999)

Table 2.2. Models (95% confidence set) of breeding dispersal probability (P_{BD}) for California spotted owls in northeastern California, 1990-2001 ($n = 535$). Models are ordered by AICc and the best model rescaled $R^2 = 0.40$.

Model	$\log(\mathcal{L})$	K	AICc	$\Delta AICc$	w_i
P_{BD} (Age class + Reproduced + Mate + Quality + Repro*Quality + Mate*Quality)	-79.05	10	158.51	0.00	0.18
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Repro*Quality + Mate*Quality + Sex*Repro)	-79.09	12	158.77	0.25	0.16
P_{BD} (Age class + Mate + Quality + Mate*Quality)	-79.55	8	159.36	0.85	0.12
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Repro*Quality + Mate*Quality)	-79.66	11	159.82	1.31	0.09
P_{BD} (Age class + Reproduced + Mate + Quality + Mate*Quality)	-80.12	9	160.58	2.06	0.06
P_{BD} (Sex + Age class + Mate + Quality + Mate*Quality)	-80.24	9	160.83	2.32	0.06
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Mate*Quality + Sex*Repro)	-80.23	11	160.97	2.45	0.05
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Repro*Quality + Sex*Repro)	-80.41	10	161.24	2.73	0.05
P_{BD} (Age class + Reproduced + Mate + Quality + Repro*Quality)	-80.59	8	161.45	2.94	0.04
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Mate*Quality)	-80.81	10	162.04	3.52	0.03
P_{BD} (Age class + Mate + Quality)	-81.05	6	162.26	3.74	0.03
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Repro*Quality)	-81.09	9	162.52	4.01	0.02
P_{BD} (Sex + Age class + Reproduced + Mate + Quality + Sex*Repro)	-81.17	9	162.68	4.17	0.02
P_{BD} (Age class + Reproduced + Mate + Quality)	-81.27	7	162.76	4.25	0.02
P_{BD} (Sex + Age class + Mate + Quality)	-81.61	7	163.43	4.91	0.02
P_{BD} (Sex + Age class + Reproduced + Mate + Quality)	-81.83	8	163.93	5.41	0.01
P_{BD} (Sex + Reproduced + Mate + Quality + Repro*Quality + Mate*Quality + Sex*Repro)	-81.93	10	164.27	5.76	0.01

Table 2.3. Parameter estimates for logistic regression model of breeding dispersal of California spotted owls in northeastern California, 1990-2001.

Parameter		Estimate	Standard error
Intercept		-1.252	0.589
Age class	S1	1.066	0.690
Age class	S2	0.380	0.546
Reproduced	0	0.390	0.395
Mate	N*	-2.151	0.431
Mate	S*	1.783	0.599
Quality		0.257	1.446
Reproduced*Quality	0	-2.519	1.269
Mate*Quality	N*	-3.762	1.520
Mate*Quality	S*	4.923	2.097

*Codes for Mate: N = No mate loss (owl was paired before dispersal);
S = owl was Single before dispersal.

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Table 2.4. Cumulative Akaike weights (w_+) of variables in models of breeding dispersal of California spotted owls in northeastern California, 1990-2001 ($n = 535$).

Variable	w_+
Mate	1.00
Quality	0.99
Age class	0.96
Reproduced	0.78
Mate * Quality	0.76
Reproduced*Quality	0.57
Sex	0.54
Sex*Reproduced	0.30

Table 2.5. Models of breeding dispersal distance (D) for California spotted owls in northeastern California, 1990-2001 ($n = 37$). Models are ordered by AICc. First and second-year subadult age classes were combined.

Model	$\log(\mathcal{L})$	K	AICc	ΔAICc	w_i
D (Pre-dispersal Territory Quality)	-46.08	3	98.89	0.00	0.425
D (Intercept only)	-47.80	2	99.94	1.05	0.251
D (Age class)	-47.58	3	101.89	3.00	0.095
D (Sex)	-47.71	3	102.15	3.26	0.083
D (Post-dispersal Territory Quality)	-47.78	3	102.30	3.40	0.077
D (Mate)	-46.66	4	102.58	3.68	0.067
D (Sex + Age class + Mate + Pre-dispersal Quality + Post-dispersal Quality)	-44.97	8	111.07	12.18	0.001

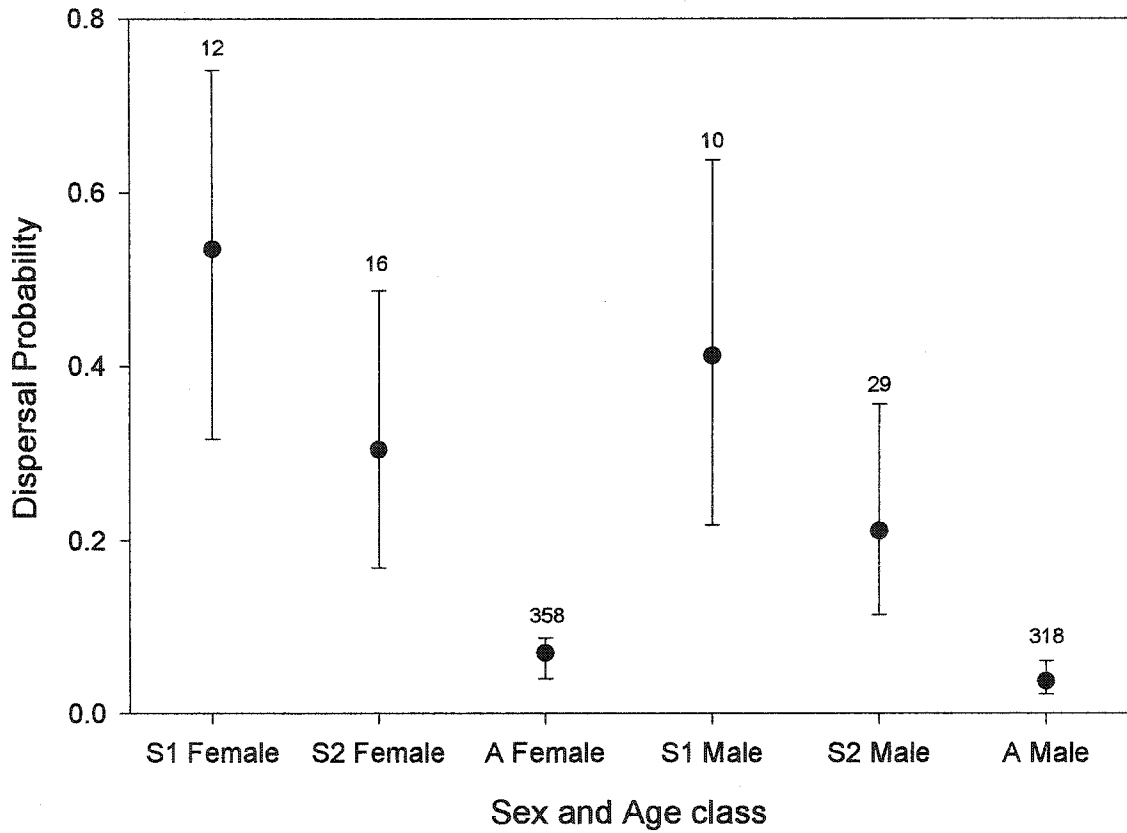


Figure 2.1. Estimated breeding dispersal probabilities of California spotted owls in northeastern California, 1990-2001. Error bars represent profile likelihood 95% confidence intervals. Key to age class: S1 = first year subadult; S2 = second year subadult; A = adult. Sample sizes appear above error bars.

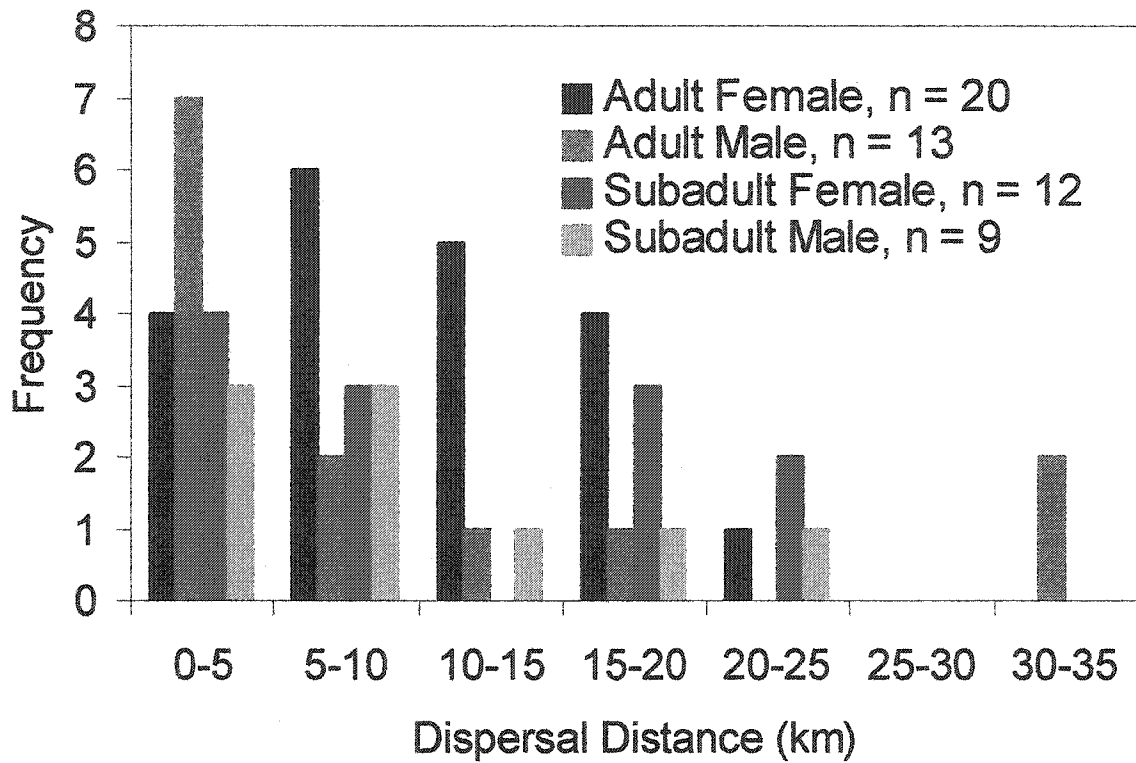


Figure 2.2. Breeding dispersal distances of California spotted owls in northeastern California, 1990-2001.

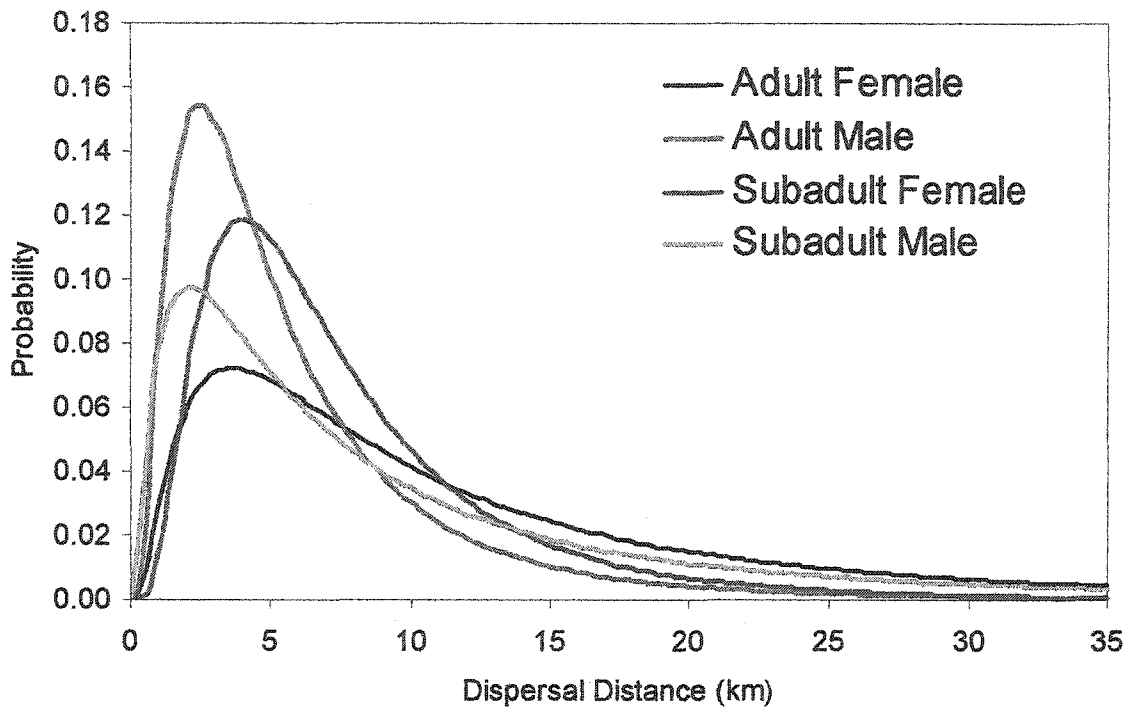


Figure 2.3. Lognormal probability density functions (maximum likelihood estimates) of breeding dispersal distance for California spotted owls in northeastern California, 1990-2001.

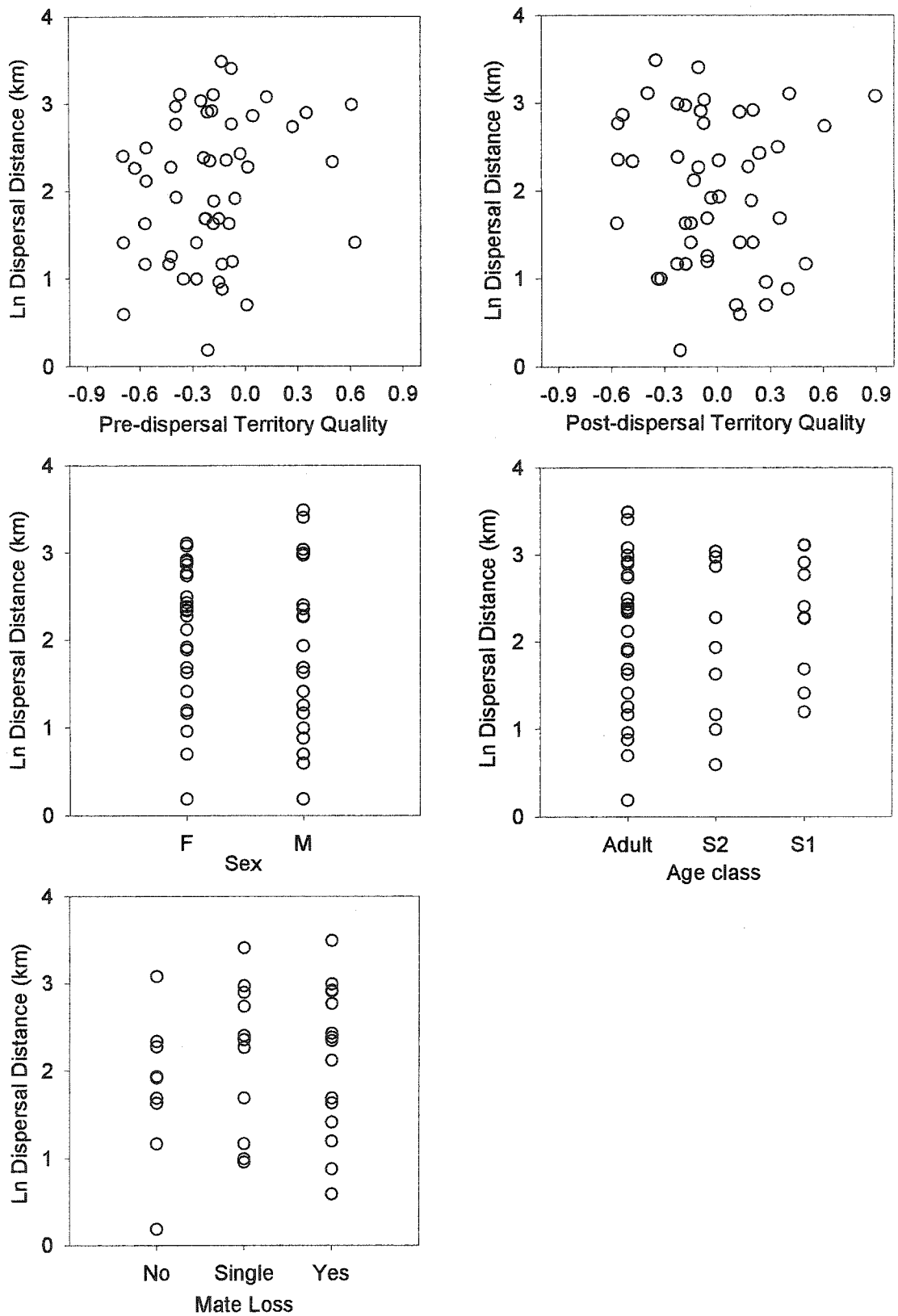


Figure 2.4. Dispersal distance (log transformed) as a function of territory quality, sex, age class, and mate loss for California spotted owls in northeastern California, 1990-2001.

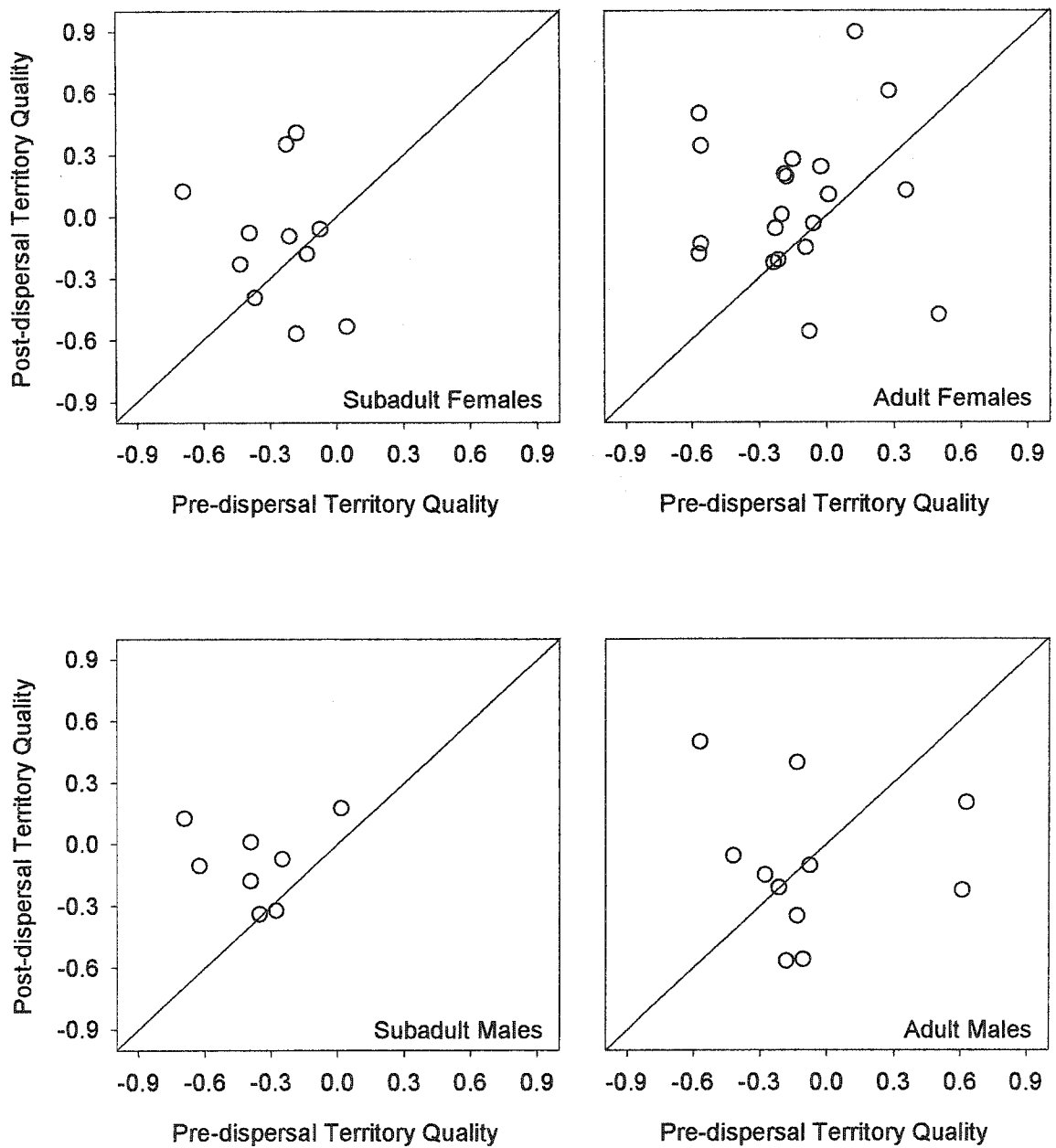


Figure 2.5. Pre- and post-breeding dispersal territory quality for California spotted owls in northeastern California, 1990-2001. Circles above the diagonal line represent owls which improved territory quality by dispersing. Circles below the diagonal line represent owls which moved to territories of lower quality.