

ASSOCIATION OF WEATHER AND NEST-SITE STRUCTURE WITH REPRODUCTIVE SUCCESS IN CALIFORNIA SPOTTED OWLS

MALCOLM NORTH, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

GEORGE STEGER, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

RENEE DENTON, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

GARY EBERLEIN, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

TOM MUNTUN, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

KEN JOHNSON, Pacific Southwest Research Station, Forestry Sciences Lab, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

Abstract: Although the spotted owl (*Strix occidentalis*) has been intensively studied, factors influencing its reproduction are not well understood. We examined a 9-year demographic study of 51–86 pairs of the California spotted owl (*S. o. occidentalis*), weather conditions, and forest structure at nest sites in oak (*Quercus* sp.) woodland and conifer forests to assess if weather or nest-site variables are associated with reproduction. Mean reproduction was highly variable between years, but within a given year was largely synchronous among all owl pairs across forest types (i.e., oak woodlands and conifer) with different prey bases. There was no significant difference in reproduction between owls on National Forest and National Park lands. In oak woodlands and conifer forest, mean fledgling production was negatively correlated with nesting period precipitation, and in conifer forests, positively correlated with April's minimum temperature. For both forest types, live-tree nests were in large (diam at breast height [dbh] > 150 cm), old trees (>225 yr) with large crowns (foliage volume >1,700 m³). Regardless of forest type, all nest sites had similar canopy cover (76%), tree density (312 stems/ha), and foliage volume (45,000 m³/ha). Nests with repeated use produced more young than nests used only 1 year. In oak woodlands, nests with higher reproduction were on shrubby, north-aspect slopes in trees or snags surrounded by a well-developed canopy. In conifer forests, reproductive success was associated with nests overtopped by a canopy with a high foliage volume. Synchronous annual reproduction and the association of nest-period weather and canopy structure with production of young, suggests that reproduction is influenced by both regional weather conditions and nest-site canopy structure, which protects fledglings from detrimental weather.

JOURNAL OF WILDLIFE MANAGEMENT 64(3):797–807

Key words: California spotted owl, canopy foliage, mixed-conifer forest, oak woodlands, owl reproduction, stand structure, *Strix occidentalis occidentalis*, weather.

The management of many western forests has been directly influenced by legal and biological requirements for maintaining viable populations of the spotted owl (Thomas et al. 1990, Verner et al. 1992a). While most of the controversy has focused on protecting the old-growth habitat associated with the owl, the long-term viability of the species will also depend on its reproductive success. It has been difficult to assess owl population trends because owls disperse over large areas and demographic studies rarely have a closed population in which a complete, long-term census has been conducted (Forsman et al. 1996). In the absence of better demographic data, identifying factors that may influence reproduction can be an important tool for inferring population response to changing environmental conditions.

Spotted owl studies have suggested several influences on reproduction including weather

(Wagner et al. 1996, Zabel et al. 1996, Franklin 1997), prey-base abundance (Forsman et al. 1984, Barrows 1985, Carey et al. 1992, Franklin 1997), habitat quality and fragmentation (Laymon 1988, Carey et al. 1992), and nest-site characteristics (Gutiérrez et al. 1992, LaHaye et al. 1997). Over the course of a 9-year demographic study, we noticed 2 trends in reproduction. Across our study area, reproductive success of all surveyed owls tended to be synchronous within any given year. The pattern of occasional good years in which almost all owl pairs produce young, interspersed with many poor years in which few owls nest or produce young, has been noted in demographic studies of the northern spotted owl (*S. o. caurina*; Forsman et al. 1996). This pattern suggested a common factor, such as weather or abundance of prey, influenced reproductive success across the study area at a regional scale.

A second trend over the 9-year study was a local effect on reproduction, where some nest sites had consistently higher reproductive success than others. Even during several low reproduction years, these nest sites continued producing young. The higher reproductive success of repeated-use nest sites suggests that a local condition (nest site or home range) may affect reproduction.

We examined California spotted owl nests and reproduction in the southern Sierra Nevada where weather and forest structure significantly differ from previous studies in northern (Solis and Gutiérrez 1990, Zabel et al. 1996, Franklin 1997) and central (Laymon 1988) California, and the Los Angeles basin mountains (LaHaye et al. 1994, 1997). Reproduction was annually censused in 2 forest types with distinct prey bases, and on National Forest and National Park lands with different management practices. Our objectives in this study were to (1) compare reproduction between land management areas and forest types with different prey bases, (2) assess if weather conditions were correlated with reproduction, (3) characterize nest-site structure for the southern Sierra Nevada, and (4) identify and quantify nest site attributes correlated with higher reproduction.

This study focussed on 2 possible influences on reproduction, when in fact many factors probably contribute to reproductive success or failure. In particular, nest predation, prey-base abundance and availability, and individual owl reproductive quality probably differ between owl territories, making it difficult to isolate the influence of weather and nest-site structure. We do not have data on nest predation or availability of prey in our study areas, and only limited information on the reproductive history of individual owls. Our study, therefore, is restricted to the potential reproductive influences we tested and does not attempt to investigate all the factors driving spotted owl reproduction.

STUDY AREAS

Spotted owls were surveyed in 2 study areas, the Sierra National Forest and Sequoia-Kings Canyon National Park. The Sierra National Forest study area encompassed 419 km² from 350 to 3,050 m elevation and surveys have identified 51 owl territories. In Sierra National Forest, most of the forest has been repeatedly thinned since the late Nineteenth Century. Although most stands have been selectively cut with dif-

ferent intensities, forest cover has not been fragmented by clearcutting. In 1994, the Sierra National Forest study area was expanded to include an adjacent area of 267 km² which contained 18 owl territories. Owl reproductive data for 1994–98 include this additional area. The Sequoia-Kings Canyon National Parks study area, approximately 30 km south of Sierra National Forest, was 343 km² and ranges from 600 to 2,750 m elevation. Owl surveys have identified 44 owl territories. This study area, for the most part, is unharvested old growth with some large stands of giant sequoia (*Sequoiadendron giganteum*).

In both study areas, forest type changes with elevation and aspect. Generally, forests from 100–1,200 m elevation are oak woodlands and oak-chaparral with an overstory mix of valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), interior live oak (*Q. wislizenii*), canyon live oak (*Q. chrysolepis*), California buckeye (*Aesculus californica*), sycamore (*Platanus racemosa*) and an understory of poison oak (*Toxicodendron diversiloba*), buckbrush (*Ceanothus cuneatus*), and whiteleaf manzanita (*Arctostaphylos viscida*). Tree density and understory cover increase with elevation, proximity to stream channels, and more northerly aspects.

From 1,200 to 1,800 m elevation, forests are dominated by ponderosa pine (*Pinus ponderosa*), but also contain sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and black oak (*Q. kelloggii*). Ponderosa pine stands have an understory of buckbrush, greenleaf manzanita (*Arctostaphylos patula*), mountain misery (*Chamaebatia foliosa*), and bitter cherry (*Prunus emarginata*). From 1,800 to 2,200 m elevation, forests are mixed conifer dominated by white fir, red fir (*Abies magnifica*), sugar pine, Jeffrey pine (*P. jeffreyi*), incense cedar, and black oak. Understory shrubs include whitethorn ceanothus (*Ceanothus cordulatus*), greenleaf manzanita, bitter cherry, and snowberry (*Symphoricarpos rotundifolius*). In both study areas, owls also used giant sequoia groves within the mixed-conifer zone. Although similar in tree and shrub composition to mixed conifer, sequoia groves have a distinct structure with high basal area, tall canopies, and low tree density. From 2,200 to 3,050 m elevation, the red fir forest type is dominated by red fir and some white fir. The understory has a sparse cover of sticky currant (*Ribes viscosissimum*) and snowberry.

METHODS

Reproduction Censuses

This study builds on an ongoing demographic study of 51–86 pairs of California spotted owls that began in 1990 (Verner et al. 1990). Beginning in April of each year, field crews located spotted owls using standard methods (Forsman 1983). Each year all new owls are captured, banded, sexed, and approximately aged (Forsman 1981). An observer imitated owl calls in each territory to elicit a response. If there was no response in a territory the site was called until 6 surveys were completed and the site was declared vacant for that year. Responding owls were systematically visited using demographic protocol (Verner et al. 1990) to determine nesting, nest location, and reproduction. Nesting visits took place from 1 March to 31 May, and reproductive success was determined by counting fledgling owls before 15 July (Steger et al. 1993). Nest trees were marked with plaques or flagging, and location was recorded using topographic maps or a geographic positioning system. When fledgling owls were located after the 15 July cutoff date they were not counted. If a territory was not called to full protocol or reproduction was not determined, the site was not counted in the annual census. Due to weather problems, the reproduction of only a few owl pairs in oak-woodland sites was surveyed in 1998, and these data were not included in calculating mean annual reproductive rate.

Nest Site Structure

For each nest tree, nest height and type (i.e., top or side cavity, platform, broom, etc.) were recorded. For live trees, the species, dbh, and crown condition (normal, broken-top, bayonet, multi-top, or dead) were recorded. Whenever possible, tree age was determined using an increment borer (snags, sequoias, and some of the largest oaks were not cored). On trees with heart rot, age was conservatively recorded as the number of all visible rings. For snags, the total height, decay class (Cline et al. 1980), and number of cavities were recorded. At each nest site, slope, aspect, elevation, distance to perennial water, and distance to the nearest large opening were measured.

To characterize the forest structure surrounding the nest, vegetation was measured in 3 nested circular plots: a 0.05-ha plot for all trees and snags ≥ 5 cm dbh, a 0.1-ha plot for all logs, and

trees and snags ≥ 50 cm dbh, and a 0.2-ha plot for all trees ≥ 80 cm and all snags ≥ 50 cm dbh (Spies and Franklin 1991, North et al. 1999). Shrub and log cover were measured along 50 m transects placed along the fall line and cross slope, and intersecting at plot center. Canopy cover for the nest area was determined by averaging 10 moosehorn readings recorded on a systematic grid surrounding the nest tree.

For every nest tree and each tree in the 0.05-ha plot, whole crown and above-nest foliage volumes were calculated. Each crown was classed as 1 of 4 solids: cone, cylinder, truncated ellipse, or umbrella shape, subtended by a cylindrical wedge if a partial crown was present. Foliage volume was calculated as a simple geometric solid using measurement of the tree's total height, height to base of the live crown, height to the partial crown, the arc of the partial crown, and 2 crown diameters (Van Pelt and North 1996, 2000). For the 0.05-ha plot, the total and above-nest foliage volume for all trees was summed to calculate a standardized canopy volume surrounding and above each nest.

Weather Data

Eighty-five of the owl nests were in conifer forests and 32 nests were in oak woodlands. Data from automated weather stations were available from several sites within the study area. We compared data from 4 recording stations and found no significant difference in measurements between stations at similar elevations but differences between oak and conifer sites. We selected 1 weather station in the conifer zone (2,100 m) at Grant Grove in Kings Canyon National Park and 1 weather station in oak woodlands (300 m) at the U.S. Forest Service District Office at Trimmer. From daily averages at both stations, monthly averages were calculated for maximum and minimum temperatures, total and average precipitation, duration of precipitation, and wind speed. The highest and lowest temperatures, greatest wind speeds, and highest single day's precipitation in each month were also used in the analysis.

Data Analysis

To assess mean reproduction by year and specific nest site, data were analyzed with 2 different methods. For the annual analysis of reproduction, the reproductive rate for each year between 1990 and 1998 was calculated by dividing the total number of young by the number of

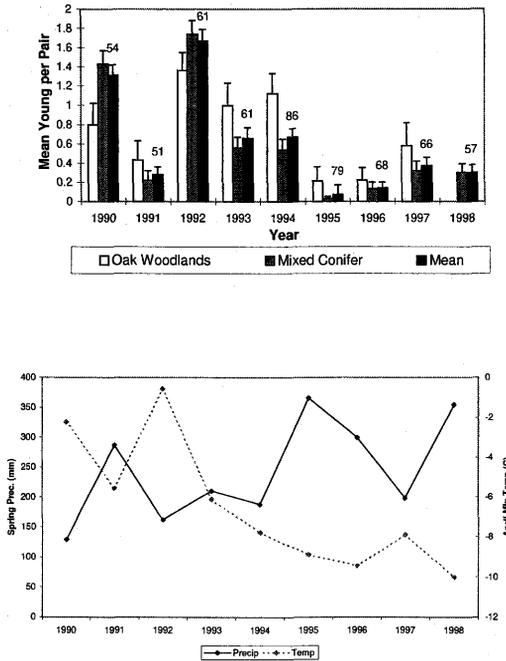


Fig. 1. Annual patterns of owl reproduction from 1990–98 in the southern Sierra Nevada for owls in oak woodlands, conifer forest and overall. Bars indicate SE with the number of owl pairs surveyed each year on top. The bottom graph shows precipitation (March through May) and minimum April temperature recorded at Grant Grove, California (2,100 m) from 1990–1998.

owl territories surveyed in 2 forest types. Mean reproduction between the oak woodland and conifer forests, and between Sierra National Forest and Sequoia–Kings Canyon National Park was compared with a paired *t*-test.

Weather data included 10 measures of temperature, precipitation, and wind speed for each month of the year and 2 seasonal summations (breeding and nonbreeding season), or 122 predictor variables for each annual reproductive rate. We followed Williams and Titus's (1988) suggestion that there should be at least 3 response data for each predictor variable in a multivariate model. We used Pearson's correlation analysis to reduce the number of weather variables and identify the 3 variables most significantly correlated with annual reproduction in oak woodland and conifer forests. In each forest type, the 3 variables identified were modeled against annual reproduction using classification and regression tree (CART) analysis. The least squared model of CART was selected with a significance level of 0.05 and a minimum node size of 2 (SYSTAT 1998).

To analyze the data for forest type and nest site differences in reproduction, a weighted reproductive value for each nest ($n = 117$) was calculated. The weighting increased the reproductive significance of nests that were successful in bad years by factoring in the overall reproductive rate for the whole study area. The weighting was calculated for each nest as number of young_{*x*}/mean reproductive rate_{*x*}, where *x* is the year when a nest produced young. For nests with >1 year of production, mean reproduction for the nest site was calculated by averaging the weighted reproduction for all years when young were produced. Mean weighted reproduction was not normally distributed, so in all analyses we used the square-root transformation, which was normally distributed.

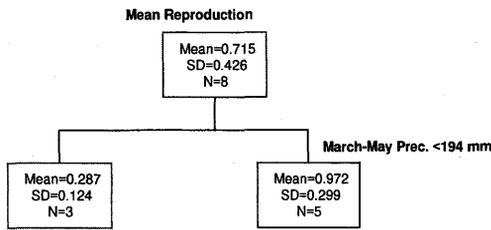
Using the data for the nest tree and the 3 nested circular plots, the following variables were calculated for each nest site: nest height and type, nest tree total height, dbh, crown form, and foliage volume, tree basal area (m²/ha), tree density (no. of stems/ha), snag volume (m³/ha), log volume (m³/ha), aspect, distance to nearest perennial water, and elevation. Aspect was transformed with a cosine function (Beers et al. 1966) and compared using the Watson-Williams test (Zar 1984). Three measures of forest canopy structure were also calculated: total foliage volume (m³/ha), foliage volume above and immediately surrounding the nest (i.e., within a 0.05-ha circle around the nest), and total canopy cover. Foliage volume was calculated following procedures in Van Pelt and North (1996, 2000).

To evaluate which structures might be associated with nest-site reproduction, each nest's mean weighted reproduction was analyzed against nest-site characteristics in separate models for oak woodland and conifer nests. For each model, nest-site variables were tested for collinearity (V.I.F. > 15; Belsley et al. 1980) and then modeled using CART.

RESULTS

For the 9 years of the demographic study, mean annual reproduction varied from 0.07 to 1.67 young per owl pair, and was either below 0.37 or above 0.67 young per pair for any given year (Fig. 1). Of 313 fledglings produced, 296 (94.6%) were from pairs where both owls were classed as adults (≥ 3 yr old). Only adult/adult pairs were used in further analyses. For adult pairs there was no correlation between fledgling

A.



B.

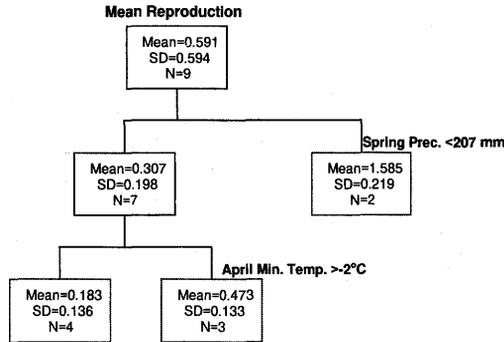


Fig. 2. Classification and regression tree analysis of weather variables correlated with annual owl reproduction in (A) oak woodlands and (B) mixed-conifer forest. The mean, standard deviation, and number of cases are shown in each box. The oak woodland analysis is for 1990-97 and the mixed-conifer analysis is for 1990-98.

production and approximate age of either parent (Spearman's rho = 0.17, P = 0.53). Annual reproduction for owls in oak woodland and conifer forests was highly correlated (Spearman's rho = 0.77, P = 0.026). There was no significant difference between mean annual reproduction in the Sierra National Forest and Sequoia-Kings Canyon National Park (P = 0.74, α = 0.05, β = 0.9).

In the Pearson's correlation analysis of weather with annual reproduction in oak woodlands, the 3 most significant variables were total March-May precipitation (the nesting period), the minimum temperature during March to May, and the duration of precipitation in May. In the CART analysis, owl pairs averaged 0.69 more fledglings in years with <19 cm of rain between March and May (Fig. 2).

The 3 most significant weather variables for owl reproduction in conifer forests were total March-May precipitation, the minimum temperature in April, and the mean temperature from March to May. In the CART analysis, annual conifer owl reproduction was significantly

Table 1. Mean weighted number of young per owl pair and number of nests, classed by years of nest use.

Number of years a nest is used	Number of nests	Mean weighted number of young/owl pair
1	76	1.61 ^a
2	30	2.54 ^{ab}
≥3	11	3.29 ^b

^{ab} Values with different superscripts are significantly different (P < 0.05, posthoc, ANOVA).

higher during years when nesting-period total precipitation was <21 cm and the minimum temperature in April was > -2°C (Fig. 2).

Nests with ≥3 yrs had more than double the weighted reproductive rate of nests used just 1 year (Table 1). Owl nests in oak-woodland sites significantly differed from conifer sites in aspect, proximity to water, and shrub cover. Conifer sites had higher tree basal area, foliage volumes, snag, and log volumes (Table 2). Nests in both forest types had 3 common characteristics: tree density, canopy cover and foliage volume.

Nest characteristics by nest-tree species indicate that giant sequoia and black oak were used in significantly higher proportion (χ² = 20.73, 0.025 < P < 0.05) than their relative abundance within all the sample plots. On average, nests were 24 m aboveground, in large (mean dbh = 157 cm), old (>227 yr) trees (Table 3). There was no significant difference in mean reproduction between platform and cavity nests (t_{0.05 (2),113} = 0.46 P = 0.83). Most (64%) conifer nest trees (including giant sequoia) had irregular (broken-off, dead, or multiple-leader) crowns and most (82%) nests were in cavities.

Table 2. Site characteristics of oak-woodland and mixed-conifer nests. Oak-woodland and mixed-conifer variables in parentheses are significantly different (P < 0.05 by Student's t-test).

Site variables	Forest type	
	Oak-woodland (n = 32)	Mixed-conifer (n = 85)
Aspect (degrees)	353	166
Distance to water (m)	73	153
Shrub cover (%)	37.2	12.8
Tree basal area (m ² /ha)	18.2	82.7
Density (stems/ha)	300	316
Canopy cover (%)	75	76.2
Foliage volume (m ³ /ha)	39,413	46,879
Above nest foliage volume (m ³ /0.05 ha)	1,302	3,253
Snag volume (m ³ /ha)	7.4	153.5
Log volume (m ³ /ha)	17.3	212.9

Table 3. Characteristics of owl nest trees. Some ages are listed as > values when the number of visible rings were counted in heart-rot affected increment cores.

Species	n	Age (yr)	dbh (cm)	Tree ht. (m)	Nest ht. (m)	Foliage volume (m ³) of nest tree	No. of irregular crowns (broken, multi-top):	Nest type			
								Platform	Top cavity	Side cavity	Unknown
<i>Abies concolor</i>	27	>241	129	43.7	29.9	1,032	25	5	7	14	1
<i>Sequoiadendron giganteum</i> ^a	19	—	461	72.8	40.1	7,414	10	0	1	18	0
Snag (mean decay class = 2)	17	—	113	33.2	24.4	—	—	1	4	12	0
<i>Quercus kelloggii</i> ^a	13	>139	91	20.9	11.9	623	9	0	1	12	0
<i>Quercus wislizenii</i>	12	—	35	13.4	9.8	377	1	12	0	0	0
<i>Pinus lambertiana</i>	8	312	103	38.1	21.6	974	5	3	2	2	1
<i>Quercus chrysolepis</i>	6	—	52	15.0	11.3	303	1	6	0	0	0
<i>Quercus douglasii</i>	5	>292	88	18.5	9.1	599	2	0	1	4	0
<i>Pinus ponderosa</i>	4	143	91	44.9	27.9	1,427	3	3	1	0	0
<i>Abies magnifica</i>	2	>292	142	50.2	33.3	1,328	2	2	0	0	0
<i>Quercus lobata</i>	1	—	103	20.3	9.0	1,472	0	0	0	1	0
<i>Platanus racemosa</i>	2	—	64	16.4	5.8	1,128	0	0	1	1	0
<i>Pinus sabrina</i>	1	110	85	37.0	32.7	1,348	0	1	0	0	0
All nests	117	>227	157	37.8	23.7	1,775	58	33	18	64	2
Oak woodland nests	32	>201	66	18.9	12.8	544	4 (13%)	20 (63%)	4 (12%)	8 (25%)	0
Mixed-conifer nests ^b	66	>229	114	36.9	24.3	965	44 (66%)	13 (20%)	13 (20%)	38 (57%)	2 (3%)

^a Species has significantly more nests than expected from forest composition ($P < 0.05$, chi-square test).

^b Does not include *Sequoiadendron giganteum* nests.

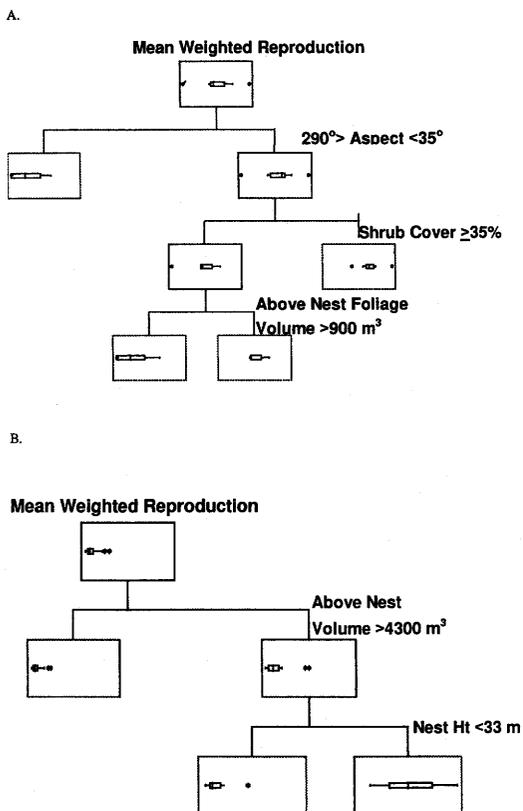


Fig. 3. Classification and regression tree analysis of nest site variables correlated with owl reproduction in (A) oak woodlands and (B) mixed-conifer forest. Within each CART node, the box indicates the 25–75 percentile of weighted reproduction values and the mean is marked with a vertical line.

Oak-woodland sites had a higher percentage of platform nests (63%), and nest trees had high foliage volumes (544 m³) for their size (mean dbh = 66 cm).

For oak-woodland nests, higher reproduction occurred on sites with a northerly aspect, shrub cover >35%, and an above-nest foliage volume >900 m³ in a 0.05-ha area surrounding the nest (Fig. 3). For nests in conifer forests, reproduction was higher on sites with above-nest foliage volume >4,300 m³/0.05 ha and in nests <33 m in height (Fig. 3).

DISCUSSION

Demographic studies of spotted owls have reported low mean annual reproductive rates but with a high degree of variability (Noon et al. 1992, Forsman et al. 1996). The 51–87 censused pairs in our study area were consistent with these trends, averaging 0.58 young per owl pair per year over the 9-year study, but ranging

from a low of 0.07 in 1995 to a high of 1.67 in 1992. The pattern that all pairs tend to have similar reproductive success or failure within a year suggests a common regional influence on spotted owl reproduction.

Fluctuations in prey abundance have been proposed as a significant and synchronizing influence on spotted owl reproduction (Forsman et al. 1984, Barrows 1985). Many owl studies in North America, Asia, and Europe have found a positive relationship between prey availability and reproduction (Lundberg and Westman 1984, Cramp 1985, Wiklund and Stigh 1986, Petty 1987, Johnsgard 1988, Verner et al. 1992b). Furthermore, several of the spotted owl's principal prey species, including the northern flying squirrel (*Glaucomys sabrinus*), may have dramatic annual population fluctuations (Garsd and Howard 1981, Fryxell et al. 1998), which could coincide with high reproduction years.

Lacking data on prey populations, we could not test the correlation between prey abundance or availability and owl reproduction. In our study area, we do know that owls in oak woodlands and conifer forest principally rely on different prey. During this study, an analysis of pellet contents by biomass found woodrats (*Neotoma* spp.) comprised 80% of the owls' diet in oak woodlands (Munton et al. 1997), and the northern flying squirrel comprised 61% of owls' diet (T. E. Munton, unpublished data) in conifer forests. The synchronous reproduction of owls in both oak woodlands and conifer forest, however, does not necessarily require different prey populations to have similar cycles. Reproduction may be influenced by many factors not measured in this study including an interaction of prey abundance, availability, and weather. During extended periods of poor weather, nests may fail because prey are less available. Prey populations may be depressed during heavy spring rains, more difficult to capture, or require greater expenditures of energy.

Mean annual reproduction was not significantly different between National Forest and National Park lands, and both areas followed the same annual patterns of fluctuation. Conifer-forest conditions differed between the 2 areas, and we expected owl reproduction would be higher in the National Park because it had more undisturbed old growth than the Sierra National Forest. The lack of a difference in reproduction between these 2 areas does not sug-

gest that forest management has no effect on owl reproduction. Studies in the Pacific Northwest have consistently found few northern spotted owls in managed, young forests (Forsman et al. 1977, 1984; Thomas et al. 1990). In the Sierra Nevada selective cutting produces a wider array of stand conditions than the clearcutting that was commonly practiced in the Pacific Northwest. Present forest structure and composition vary by each stand's history of thinning prescriptions and fire intensity. Thinning has not fragmented forest cover, and dispersed pockets of large, old trees are common in the Sierra National Forest. Although mean reproduction did not differ, owl density was higher in Sequoia-Kings Canyon National Parks (12.8 pairs/100 km²) than in the Sierra National Forest (10.0 pairs/100 km²).

Weather conditions during owl nesting were highly correlated with annual reproduction in both oak woodland and conifer forests. All March-May precipitation and temperature variables were significantly correlated with reproduction, indicating that the pattern of weather during the nesting season possibly influenced reproduction in both forest types. Reproduction was higher in years when the March-May precipitation total was <194 mm in oak woodlands (50 yr mean = 188 mm, SD = 167 mm) and <207 mm in conifer forest (50 yr mean = 317 mm, SD = 265 mm). Two years during the study period with low reproduction, 1995 and 1998, were El Niño events when precipitation is higher and spring temperatures lower than normal in California. Studies of the northern spotted owl in northern California and southern Oregon suggested that rainfall during the nesting period may adversely affect reproduction (Wagner et al. 1996, Zabel et al. 1996, Franklin 1997). Studies of several predatory birds have found a negative affect of nesting-season rainfall on reproduction (Newton 1979, 1986, Mearns and Newton 1988, Olsen and Olsen 1989, Koszrzewa and Koszrzewa 1990, Newton et al. 1993). Newton (1979, 1986) has suggested that rain may decrease foraging success or increase energy requirements, thereby reducing reproduction in some birds.

Although our analysis found a strong association between weather and reproduction, isolating the particular nesting-weather variable which has the greatest impact on reproduction is difficult with only 8-9 years of data. It will take several decades of data to gain enough sta-

tistical power to precisely identify key climatic factors affecting reproduction. In the interim, the CART analysis gives some general guidelines for how weather may affect reproduction.

Some nests consistently had higher reproductive success than others, possibly due to habitat differences within owl territories, nest predation, breeding quality, or nest location. Reproduction at nests used ≥ 3 years was significantly higher than single-use nests. Of the 41 nests with ≥ 2 years of use, 78% were in home ranges where other nest locations were tried before the owl pair settled on the return site location. Of these other single-use nest locations, most either produced no young or produced a single young in a good year. This combination of low reproduction at single-use nest sites and higher reproduction at repeated-use sites within the same territory, suggests that reproduction may be influenced by more than just territory quality.

Owl reproduction at a nest may be influenced by at least 2 factors we did not analyze in this study. For nest failures, we do not have data on the stage of failure, the cause, or if nest predation was a factor. Forsman et al. (1984) documents 2 cases of nest predation in 70 northern spotted owl nests they surveyed, but there is little information on how widespread nest predation is among different owl subspecies or geographic areas. A second factor not assessed in this study is the interaction of owl breeding history and territory quality. In many bird species, highly productive individuals often occupy the best territories, making it difficult to distinguish whether a site's reproduction is due to the habitat or the individual bird (Brooke 1978, Findlay and Cooke 1982, Newton 1989). There was too little turnover of either male or female owls at the most productive nest sites to analyze whether reproduction significantly changed with new individuals. Of the 12 females and 10 males that used >1 nest site, individuals were not consistently either good or poor reproducers.

Oak-woodland nests were usually in dense, brushy riparian zones with high canopy cover, foliage volume, and tree density. Nests were predominantly stick platforms in large oaks on north-aspect slopes. Conifer nest sites had high basal area, low tree density, and high above-nest foliage volumes. Nests were often in a patch of the oldest and largest trees in the immediate area, and on average were in a low, side cavity of an old irregular-top tree. Many nests on the

Sierra National Forest were located in the cavities of large black oaks, a noncommercial species often left during past thinnings.

Oak woodland and conifer forests have very distinct structure and composition, yet nest sites in both forests had 3 common features: canopy cover, tree density, and foliage volume. Owl nests were consistently located in sites with 75% canopy cover, 300 stems/ha, and 40,000 m³/ha of foliage volume. Because these conditions were consistent across such different forests, canopy cover, tree density and foliage volume could indicate basic nest-site conditions selected by owls. The 3 variables provide a relative measure of how much forest cover surrounds a location. Owls could select these sites for a variety of reasons including predator protection, nest availability, or microclimate conditions.

For owls nesting in oak-woodlands, aspect, shrub cover, and foliage volume above the nest were most highly correlated with successful reproduction. Although these conditions may provide cooler microsites than surrounding oak-woodland habitat, Verner et al. (1992b) have questioned whether forest habitat is selected to avoid heat stress. Northern aspects and high shrub cover are indicative of areas with dense canopy cover along intermittent and perennial stream channels. The mean canopy cover of 75% at these nests is much higher than average for oak woodlands (Griffin 1988). Reproductive nests were overtopped by large foliage volumes in the nest tree or surrounding trees (all trees within 0.05 ha). These conditions may favorably modify microclimatic conditions for open, platform-nesting owls. If nesting-period precipitation negatively affects reproduction, high canopy cover and foliage volume may reduce the amount of throughfall precipitation (Chen et al. 1992).

In conifer forests, higher reproduction was associated with nests surrounded by high foliage volumes. Nests closer to the ground are overtopped by more foliage. Above-nest foliage volumes were greater than 4,300 m³ within a 0.05-ha circle surrounding the most productive nests. If precipitation and minimum temperatures during nesting affect owl reproduction, stands with high foliage volumes above the nest may help reduce throughfall precipitation and wind penetration, and may also buffer minimum temperatures (Chen et al. 1999). Moving from edge to interior forest, minimum temperatures

become warmer as forest canopy cover and stem density increase (Chen et al. 1993a,b).

MANAGEMENT IMPLICATIONS

Nest trees selected by owls in this southern Sierra Nevada study area were consistent with patterns noted in northern and central California studies (Gutiérrez et al. 1992). Nest trees on average are very large, old conifers with broken tops or irregular crowns. Current National Forest management practices may not adequately provide for these types of trees. In thinning operations, wolf trees (i.e., broken-off or multi-topped crown) are usually selected for harvest to remove defective trees from a stand. Another common management practice, group selection, manages a forest watershed by harvesting all trees in 0.8-ha blocks or groups, on a 200-year rotation. This would dramatically reduce the number of potential nest trees if mean nest tree age is >227 years.

The possible interaction of weather and nest-site structure on owl reproduction suggests forest managers should be cautious about reducing canopy volume in potential owl nesting areas. Retaining groups of large, old, high crown-volume trees may be needed to maintain the number of potential owl nesting sites in a forest. Owl nests in the Sierra National Forest were consistently located in these types of patches, particularly when the surrounding forest was heavily thinned. These nest-site conditions could be important for spotted owl reproduction in California if the frequency of El Niño events increases with global warming (Timmermann et al. 1999).

Spotted owl reproduction is probably influenced by many factors, including the weather and nest-site variables analyzed in this study. Prey abundance, foraging conditions, and individual breeding history may also affect regional and local owl reproduction. In our study area, however, reproduction was highly synchronous for owls in forest types with different prey bases and under different management regimes affecting foraging conditions. Owl pair reproduction varied with nesting-period precipitation and nest-site structures that can modify microclimate conditions.

ACKNOWLEDGMENTS

We thank B. Benson, B. Oakley, and the many field technicians who through the 9 years of this study helped collect data, often under

difficult conditions. We thank J. Verner, Pacific Southwest Research Station, Fresno, California for many helpful suggestions during the study and a review of this manuscript, and R. Gutiérrez and Z. Peery, Humboldt State University, Arcata, California for comments on weather variables and spotted owl reproduction. We appreciate the cooperation, assistance and weather data provided by Sierra National Forest and Sequoia-Kings Canyon National Parks personnel.

LITERATURE CITED

- BARROWS, C. W. 1985. Breeding success relative to fluctuations in diet for spotted owls in California. Pages 50–54 in R. J. Gutiérrez and A. B. Carey, technical editors. Ecology and management of the spotted owl in the Pacific Northwest. U.S. Forest Service General Technical Report PNW-185.
- BEERS, R. W., P. E. DRESS, AND L. C. WENSEL. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691–692.
- BELSLEY, D. A., E. KUH, AND R. E. WELSCH. 1980. Regression diagnostics: identifying influential data and sources of collinearity. John Wiley & Son, New York City, New York, USA.
- BROOKE, J. DE L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx shearwater *Puffinus puffinus*. *Journal of Animal Ecology* 47:477–495.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2:387–396.
- _____, _____, AND _____. 1993a. An empirical model for predicting diurnal air-temperature gradients from edge into old-growth Douglas-fir forest. *Ecological Modeling* 67:179–198.
- _____, _____, AND _____. 1993b. Contrasting microclimates among clearcut, edge, and interior old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219–237.
- _____, S. C. SAUNDERS, T. R. CROW, R. J. NAIMAN, K. D. BROSOFSKE, G. D. MROZ, B. L. BROOKSHIRE, AND J. F. FRANKLIN. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288–297.
- CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:773–786.
- CRAMP, S., editor. 1985. *Handbook of the birds of Europe, the Middle East and North Africa*. Volume 4. Oxford University Press, Oxford, England.
- FINDLAY, C. S., AND F. COOKE. 1982. Breeding synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). 1. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. *Evolution* 36:342–351.
- FORSMAN, E. D. 1981. Molt of the spotted owl. *Auk* 98:735–742.
- _____. 1983. Methods and materials for locating and studying spotted owls. U.S. Forest Service General Technical Report PNW-162.
- _____, S. DESTEFANO, M. G. RAPHAEL, AND R. J. GUTIÉRREZ. 1996. Demography of the northern spotted owl. *Studies in Avian Biology* 17:1–122.
- _____, E. C. MESLOW, AND M. J. STRUB. 1977. Spotted owl abundance in young versus old-growth forests, Oregon. *Wildlife Society Bulletin* 5:43–47.
- _____, _____, AND H. M. WRIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87.
- FRANKLIN, A. B. 1997. Factors affecting temporal and spatial variation in northern spotted owl populations in northwest California. Dissertation, Colorado State University, Fort Collins, Colorado, USA.
- FRYXELL, J. M., J. B. FALLS, E. A. FALLS, AND R. J. BROOKS. 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology* 79:213–225.
- GARS, A., AND W. E. HOWARD. 1981. A 19-year study of microtine fluctuations using time-series analysis. *Ecology* 62:930–937.
- GRIFFIN, J. R. 1988. Oak woodland. Pages 383–416 in M. Barbour and J. Major, editors. *Terrestrial vegetation of California*. California Native Plant Society, Special Publication Number 9, Sacramento, California, USA.
- GUTIÉRREZ, R. J., J. VERNER, K. S. MCKELVEY, B. R. NOON, G. N. STEGER, D. R. CALL, W. S. LAHAYE, B. B. BINGHAM, AND J. S. SENSER. 1992. Habitat relations of the California spotted owl. Pages 79–98 in J. Verner, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. *The California spotted owl: a technical assessment of its current status*. U.S. Forest Service General Technical Report GTR-133.
- JOHNSGARD, P. A. 1988. *North American owls: biology and natural history*. Smithsonian Institution Press, Washington, D.C., USA.
- KOSTRZEWA, A., AND R. KOSTRZEWA. 1990. The relationship of spring and summer weather with density and breeding performance of the buzzard *Buteo buteo*, goshawk *Accipiter gentilis* and kestrel *Falco tinnunculus*. *Ibis* 132:550–559.
- LAHAYE, W. S., R. J. GUTIÉRREZ, AND H. R. AKCAKAYA. 1994. Spotted owl metapopulation dynamics in southern California. *Journal of Animal Ecology* 63:775–785.
- _____, _____, AND D. R. CALL. 1997. Nest-site selection and reproductive success of California spotted owls. *Wilson Bulletin* 109:42–51.
- LAYMON, S. A. 1988. *Ecology of the spotted owl in the central Sierra Nevada, California*. Dissertation, University of California, Berkeley, California, USA.
- LUNDBERG, A., AND B. WESTMAN. 1984. Reproductive success, mortality and nest site requirements of the Ural owl *Strix uralensis* in central Sweden. *Annales Zoologici Fennici* 21:265–269.

- MEARNS, R., AND I. NEWTON. 1988. Factors affecting breeding success of peregrines in south Scotland. *Journal of Animal Ecology* 57:903-916.
- MUNTON, T. E., K. D. JOHNSON, G. N. STEGER, AND G. E. EBERLEIN. 1997. The diet of California spotted owls in riparian deciduous and oak habitats of the southern Sierra Nevada. Pages 683-687 in N. H. Pillsbury, J. Verner, and W. D. Tietje, technical editors. Proceedings of a symposium on oak woodlands: ecology, management and urban interface issues. U.S. Forest Service General Technical Report PSW-160.
- NEWTON, I. 1979. Population ecology of raptors. T. and A. D. Poyser, Berkhamsted, England.
- . 1986. The sparrowhawk. T. and A. D. Poyser, Calton, England.
- . 1989. Synthesis. Pages 441-469 in I. Newton, editor. Lifetime reproduction in birds. Academic Press, San Diego, California, USA.
- , I. WYLLIE, AND P. ROTHERY. 1993. Annual survival of sparrowhawks *Accipiter nisus* breeding in three areas of Britain. *Ibis* 135:49-60.
- NOON, B. R., K. S. MCKELVEY, D. W. LUTZ, W. S. LAHAYE, R. J. GUTIÉRREZ, AND C. A. MOEN. 1992. Estimate of demographic parameters and rates of population change. Pages 175-186 in J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report PSW-133.
- NORTH, M., J. FRANKLIN, A. CAREY, E. FORSMAN, AND T. HAMER. 1999. Forest structure of the northern spotted owl's foraging habitat. *Forest Science* 45:520-527.
- OLSEN, P. D., AND J. OLSEN. 1989. Breeding of the peregrine falcon *Falco peregrinus*: III. Weather, nest quality, and breeding access. *Emu* 89:6-14.
- PETTY, S. J. 1987. Breeding of tawny owls (*Strix aluco*) in relation to their food supply in an upland forest. Pages 167-169 in D. J. Hill, editor. Breeding and management in birds of prey. University of Bristol Publishing Company, Bristol, England.
- SOLIS, D. M., JR. AND R. J. GUTIÉRREZ. 1990. Summer habitat ecology of northern spotted owls in northwestern California. *Condor* 92:739-748.
- SPIES, T. A., AND J. F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-110 in L. F. Ruggiero, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report PNW-285.
- STEGER, G. N., T. E. MUNTON, AND J. VERNER. 1993. Preliminary results from a demographic study of spotted owls in Sequoia and Kings Canyon National Parks, 1990-1991. Pages 83-92 in S. D. Veirs, Jr., T. J. Stohlgren, and C. Schowewald-Cox, editors. Proceedings of the fourth conference on research in California's National Parks. Cooperative Park Studies Unit, University of California, Davis, California, USA.
- SYSTAT. 1998. SYSTAT Statistics. SPSS, Chicago, Illinois, USA.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. Report of the interagency committee to address the conservation strategy of the northern spotted owl. U.S. Forest Service, Pacific Northwest, Portland, Oregon, USA.
- TIMMERMANN, A., J. OBERHUBER, A. BACHER, M. ESCH, M. LATIF, AND E. ROECKNER. 1999. Increased El Nino frequency in a climate model forced by future greenhouse warming. *Nature* 398:694-697.
- VAN PELT, B., AND M. NORTH. 1996. Measuring canopy structure in Pacific Northwest old-growth forests using a stand-level crown model. *Northwest Science* 70:15-30.
- , AND ———. 2000. Testing a ground-based canopy model using the Wind River canopy crane. Selbyana, Australia.
- VERNER, J., G. N. STEGER, D. A. LEAL, AND T. E. MUNTON. 1990. Annual progress report 1990, part 2: demography of spotted owls in the Sierra National Forest and Sequoia and Kings Canyon National Parks. U.S. Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- , K. S. MCKELVEY, B. R. NOON, R. J. GUTIÉRREZ, G. I. GOULD, JR., GORDON I. AND T. W. BECK, editors. 1992a. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report, PSW-133.
- , R. J. GUTIÉRREZ, AND G.I. GOULD, JR. 1992b. The California spotted owl: general biology and ecological relations. Pages 55-78 in J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr. and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report PSW-133.
- WAGNER, F. F., E. C. MESLOW, G. M. BENNETT, C. J. LARSON, S. M. SMALL, AND S. DESTEFANO. 1996. Demography of the northern spotted owl: Southern Cascades and Siskiyou Mountains, Oregon. *Studies in Avian Biology* 17:67-76.
- WIKLUND, C. G., AND J. STIGH. 1986. Breeding density of snowy owls *Nyctea scandiaca* in relation to food, nest sites and weather. *Ornis Scandinavica* 17:268-274.
- WILLIAMS, B. K., AND K. TITUS. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. *Ecology* 69:1275-1285.
- ZABEL, C. J., S. E. SALMONS, AND M. BROWN. 1996. Demography of the northern spotted owl: coastal mountains of southwestern Oregon. *Studies in Avian Biology* 17:77-82.
- ZAR, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Received 6 July 1999.

Accepted 19 January 2000.

Associate Editor: Sullivan.