FOREST STAND CHARACTERISTICS AND REPRODUCTION OF NORTHERN SPOTTED OWLS IN MANAGED NORTH-COASTAL CALIFORNIA FORESTS

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Abstract: We monitored reproductive success of northern spotted owls (*Strix occidentalis caurina*) at 51 sites on Simpson Timber Company's (STC) managed, young-growth forests in northwestern California from 1991 to 1995. We compared habitat characteristics between sites with high and low fecundity at 5 spatial scales (concentric circles of 7, 50, 114, 203, and 398 ha), using 2 stratifications of annual reproductive success (upper 50% vs. lower 50%, and upper 25% vs. lower 75% of the proportion of years when ≥ 1 owlet fledged). Habitat features included number of residual trees per hectare and mean proportion of 6 categories of stand age and 4 categories of basal area. Using the 50th percentile categories, we found there were higher proportions of age class 21-40 years and basal area classes 23-45 and 46-69 m^2/ha ($P \leq 0.05$) but lower proportions of recent clearcuts (0-5 yr) and basal area >69 m^2/ha ($P \leq 0.05$) at sites with high reproductive success. Using the upper 25% and lower 75% categories, we found there were higher proportions of basal area class 23-45 m^2/ha, lower proportions of 61-80-year-old stands, and more residual trees per hectare at sites with high reproductive success ($P \leq 0.05$). We also compared random sites to occupied sites via the above parameters. Spotted owl sites contained lower proportions of basal area class <23 m^2/ha and greater proportions of class >69 m^2/ha than did random sites ($P < 0.05$). There was less young forest (6-40 yr) and more forest of age class 41-60 years at spotted owl than at random sites ($P < 0.05$). Low prey abundance around spotted owl nest sites, roost sites, or both may explain why older stands with more basal area were found in higher proportions at sites with lower fecundity. Spotted owls that chose younger stands with smaller trees may have benefited from higher woodrat (*Neotoma fuscipes*) availability in young stands. Managing habitat by retaining residual trees and limiting clearcutting to at least 1.1 km beyond nest sites may prove useful in increasing reproductive success of northern spotted owls.

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The northern spotted owl (hereafter, spotted owl) has been the focus of intensive research for over 2 decades. Most studies have centered around issues of habitat selection, home range size, food habits, or population viability (e.g., Forsman et al. 1984, Carey et al. 1990, Zabel et al. 1995, Forsman et al. 1996, Noon and McKelvey 1996). Studies of habitat selection have shown that spotted owl nests are found primarily in late seral stage (>200 yr old) forests characterized by multiple canopy layers and a heterogeneous structure not typically found in young forests (Barrows 1981, Forsman et al. 1984, Solis and Gutiérrez 1990, Ripple et al. 1991, Lehmkuhl and Raphael 1993, Hunter et al. 1995, Meyer et al. 1998). Although nesting habitat data suggest habitat preferences (LaHaye 1988, Buchanan et al. 1995), there is little indication if preferred habitats are associated with increased reproductive success of spotted owls. To better understand the habitat requirements of this federally listed threatened species (Federal Register 1990), it is essential to evaluate the association of habitat with fecundity.

There have been few attempts to isolate and quantify the habitat components that enhance reproduction in spotted owls. Meyer et al. (1998) found positive correlations between spotted owl reproduction and fractal dimension, number of old-growth patches, proportion of hardwoods, and a combination of distance to nearest spotted owl pair and density of spotted owls around a site. Ripple et al. (1997) found that reproductive success was correlated with old conifer forests (≥ 50 cm diameter at breast

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height [dbh]); however, years associated with major habitat changes due to logging were excluded from analysis. LaHaye et al. (1997) found nest productivity of California spotted owls (S. o. *occidentalis)* was higher in low-elevation oak *(Quercus chrysolepis*)-big-cone fir *(Pseudotsuga macrocarpa)* forests than in high-elevation mixed conifer forests *(Pinus jeffreyi, P. ponderosa, P. lambertiana, Abies concolor)* or midelevation mixed conifer-hardwood forests.

Lehmkuhl and Raphael (1993) concluded that pair status could not be predicted by landscape fragmentation indices based on habitat patterns around single and paired spotted owl locations. This inability to predict pair status from habitat could mean that spotted owl mate selection (and possibly reproduction) is not related to habitat patterns. However, because spotted owls attract a mate to a previously established territory (Verner et al. 1992), the poor predictive quality of habitat may simply indicate that a pair's territory reflects a single spotted owl's habitat choice, or that mate quality is more important than habitat quality.

Private lands owned by STC in Humboldt and Del Norte counties of northwestern California provided an opportunity to examine this aspect of spotted owl ecology in an intensively managed forest. Unlike most spotted owl study areas, STC's property is characterized by managed, young-growth stands. Less than 1% of the area is classified as old growth (>200 yr old). In 1990-91, 83% of spotted owl pairs *(n* = 60) nested in 35-80-year-old forests (Folliard 1993).

Coastal forests of northern California are characterized by conditions that encourage rapid regeneration of cleared stands (Thomas et al. 1990), and spotted owls occupy habitat in younger age classes than observed elsewhere. The structure that characterizes these managed, young-growth forests as suitable spotted owl habitat has yet to be identified at a scale larger than the microhabitat level (see Folliard 1993). Our objectives were 2-fold. First, we attempted to quantify habitat variables that allow spotted owls to live in a continuously disrupted environment by comparing pair and roost sites to randomly selected sites on the landscape. Second, because the presence of spotted owls does not indicate successful reproduction of those owls, our study was designed to isolate those qualities of younger forests that were associated with successful reproduction. By testing random locations against those of reproductively successful spotted owls, we discovered new information concerning habitat that may be influencing spotted owl fecundity.

STUDY AREA

The study area was limited to STC lands located in the Northern California Coast Range physiographic province (Thomas et al. 1990) in Humboldt and Del Norte counties (Fig. 1). Within this area, STC owns approximately 120,000 ha of land in dispersed parcels ranging from 16 to 20,200 ha. These lands lie mainly within 32 km of the coast but extend up to 85 km inland. The area is dominated by 3 forest types: (1) coastal redwood *(Sequoia sempervirens),* (2) mixed redwood and Douglas-fir *(Pseudotsuga menziesii),* and (3) mixed Douglas-fir and oak woodlands (Zinke 1988). Species characterizing the oak woodlands include tanoak *(Lithocarpus densiflorus),* California black oak *(Quercus Kelloggii),* and Oregon white oak (Q. *garyana).* Many of the redwood and Douglas-fir stands also contain large components of hardwoods such as tanoak, big-leaf maple *(Acer macrophylum),* madrone *(Arbutus menziesii),* California bay *(Umbellularia californica),* and red alder *(Alnus rubra).*

Old-growth forests on the study area have been logged almost completely, leaving young seral stage (second and third growth) forests, the oldest of which are approximately 80-90 years old. Some stands contained scattered larger trees left for various reasons during past logging operations (low merchantability and inaccessibility). Currently, STC uses clearcutting with occasional select harvesting as their primary harvest method.

The climate is maritime and characterized by cool summers and mild, wet winters. High humidity and fog are common along the coast. Average annual rainfall ranges from 102 cm in the drier, inland areas, to 203 cm near the coast (Zinke 1988). Annual precipitation along the coast was 64 cm in 1991, 56 cm in 1992, 112 cm in 1993, 75 cm in 1994, and 133 cm in 1995 (National Weather Service, Eureka, California, unpublished data). Elevations range from sea level to approximately 900 m, and the topography is characterized by steep slopes and rugged terrain.

METHODS

Selection of Random and Spotted Owl Sites

We determined spotted owl locations and reproductive status from March through August

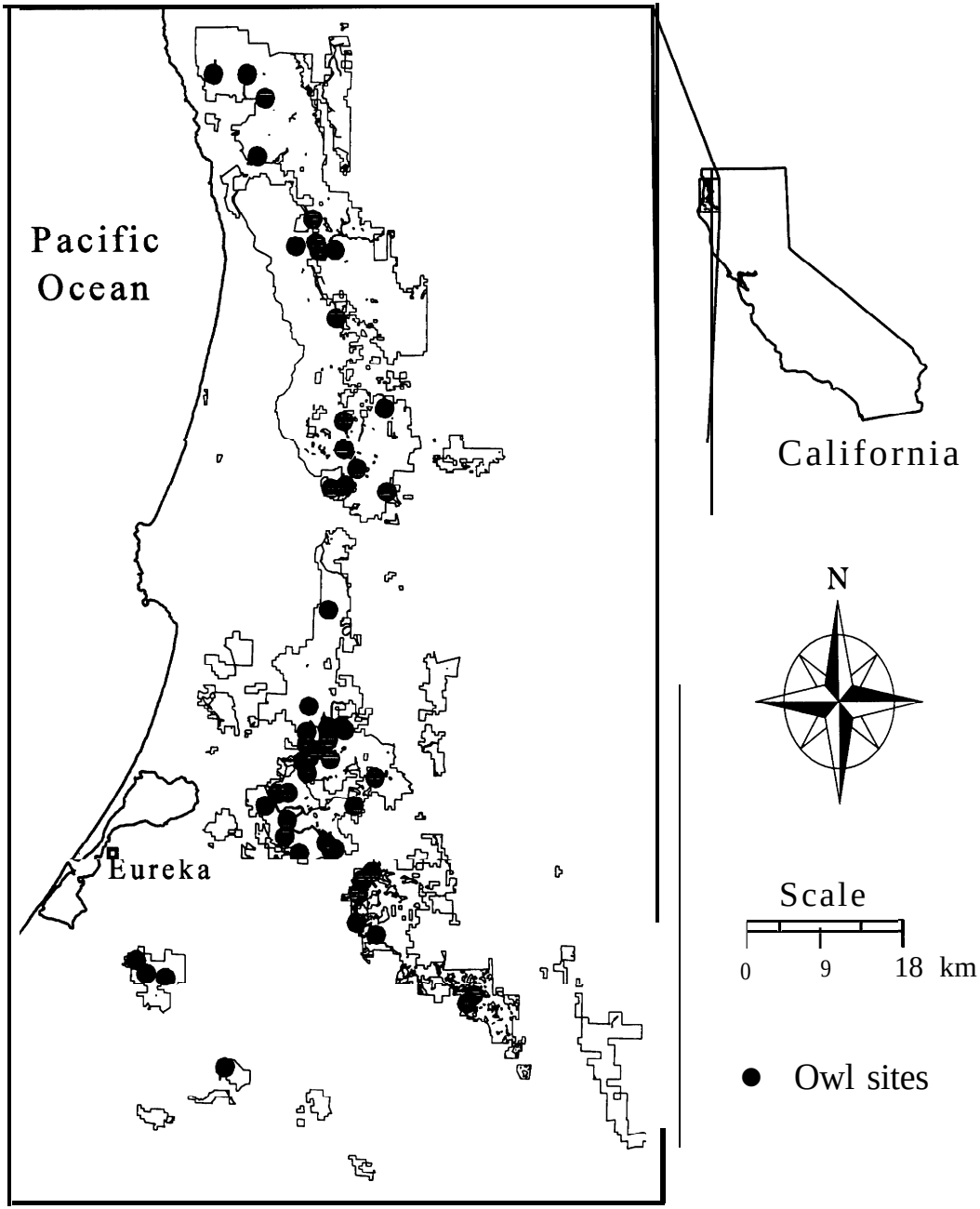

Fig.1. Map of Simpson Timber Company (STC) study area, northern California, showing distribution of 51 northern spotted owl pair locations. Spotted owl sites are scaled at 398 ha. Irregular polygons represent STC ownership.

1991-95. Surveys, census protocol, and unique color banding of juvenile and adult birds began in 1990, but standardized efforts did not begin until 1991. We recorded 262 spotted owl sites during the 5-year study period. We selected a subset of these sites based on the following criteria: (1) continuously surveyed from 1991 to 1995, and (2) occupied by a pair for at least 1 of 5 years (regardless of reproductive status). Sixty-eight sites satisfied these criteria, but because STC's Geographic Information System (GIS) data were limited to STC ownership,

spotted owl sites on the edge of STC property could not be analyzed. Useable sites were limited to those containing ≥75% of their area within STC property when a 398-ha circle (1.1-km radius) was drawn around the site center. For analysis, we used the 51 sites that met these criteria.

We generated 51 random Universal Transverse Mercator (UTM) coordinates to establish center points (site centers) of random sites. Site centers were positioned in forested habitat only (stands >6 yr old). As with spotted owl sites, we limited random sites to those that contained 75% of their area within STC property when a 398-ha circle was drawn around the site center. We analyzed spotted owl and random sites with respect to habitat characteristics at 5 spatial scales: circles of 7, 50, 114, 203, and 398 ha, with corresponding radii measuring 0.15, 0.40, 0.60, 0.80, and 1.1 km. We chose the largest and smallest scales because California regulations (California Department of Forestry and Fire Protection 1997:81--83) require spotted owl surveys to be conducted within 1.1 km of a proposed timber harvest plan, and functional nesting habitat must be maintained within 0.15 km of the active nest site or pair activity center. We selected the second largest scale, 0.80-km radius, because STC evaluates the effect of timber harvesting on spotted owls at this level. Finally, we chose the next 2 scales to provide a progressively smaller sequence to examine habitat.

Reproductive Status of Spotted Owls

We classified spotted owls as paired by observing a male and female in close proximity (<400 m) of each other in any of the following contexts: roosting, vocalizing, nesting, delivering prey, or tending young. To establish if pairs nested, we visited spotted owl pairs at least twice when the first visit was before May, or if pair status was uncertain after the first visit. A minimum of 4 mice was given to the pair during each site visit, and the pair was classified as nesting if an adult delivered a mouse to the nest or if the female was observed on the nest.

For each year, we assigned all spotted owl sites to 1 of 3 categories of reproductive success: (1) unsuccessful, (2) successful, or (3) undetermined. Categorization of successful reproduction required the observation of a fledgling (defined as a chick out of the nest). Surveys to establish reproductive success were conducted from first fledging, usually early June until 31 August. Two visits (with the minimum 4 mice protocol) were required for each nesting pair unless 2 juveniles were found on the first visit (a brood of 3 has never been observed in the study area). We visited pairs classified as nonnesting once after 1 May to ensure the initial assessment was correct and to check for late nesting.

Habitat Mapping

Extensive forest inventorv data were continually collected and input into an ORACLE database (Oracle Corporation 1990) for calculating timber volume and estimating harvestable area. Timber cruises provided data on basal area and number of residual trees, and stand ages were calculated from harvest dates. Cruise data have been collected since 1969 and were taken with a series of transect strips and variable-radius plots (Bell and Dilworth 1988) at 40.2-m intervals. Strips were spaced 201.2 m apart, and measurements included timber volume, stand structure, species diversity, and understory vegetation. Simpson Timber Company cruises approximately 2,400 ha/year, and growth modeling (a standard mensuration technique) was used to extrapolate the remaining inventory of the current year. Residual trees were defined as remnant trees from past logging operations. These trees ranged from large old-growth to relatively young trees not merchantable during the initial harvest; residual trees were conspicuously larger and older than the predominant component of the surrounding stand. The number of residual trees of all species at each spatial scale was calculated by multiplying the number of residual trees per hectare for each polygon (stand) by the size of the polygon and summing across polygons. All tree species were used in this calculation.

We distinguished forest stands based on age, and we drew polygons around each unique forest stand. Data on basal area and number of residual trees for each stand were taken from the STC database and attached to each polygon's attribute file for analysis. Simpson Timber Company uses Intergraph, a CAD-based system, which is integrated with the GIS system, Modular Graphics Environment 5.0 (Intergraph Corporation 1994). Data were converted for use with ARC/INFO version 7.0.4 (Environmental Systems Research Institute, Redlands, California, USA) and were analyzed via hardware from

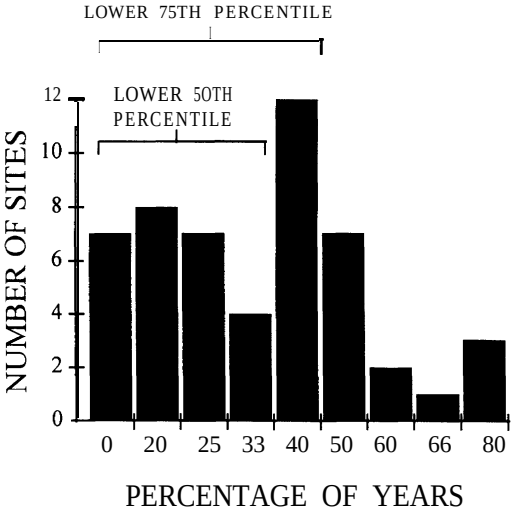

Fig. 2. Percentage of years ≥1 owlet fledged from 51 northern spotted owl sites on Simpson Timber Company property, northern California, 1991-95. Percentages excluded years when reproductive success was undetermined.

the U.S. Forest Service Pacific Southwest Research Station. Only the most recent year's (1995) GIS data were available for analysis. Landscape data from a single year were considered adequate because cumulative harvest by clearcutting had involved only 1.3% of the area within the 51 398-ha spotted owl circles during 1991-95. In addition, these clearcuts were relatively small in size (10.51 ± 0.75 ha; $\bar{x} \pm$ SE).

Spotted owls often nest in the same general area from year-to-year (Forsman et al. 1984); thus, nest locations between years may not be independent. To avoid pseudoreplication, we used a single location for each spotted owl site to evaluate habitat. Guidelines for choosing a location from 5 years of study were adopted from the U.S. Fish and Wildlife Service spotted owl survey guidelines (U.S. Department of the Interior. 1991. Final draft of spotted owl survey guidelines, unpublished report. U.S. Fish and Wildlife Service, Portland, Oregon, USA). The hierarchy of locations began with the most recent year's nest location. If no nest was located but fledglings were found, we selected the most recent year with the earliest diurnal location among those locations found within 2 months of fledging (31 Jul or earlier). In the event no nest or fledglings were found, we used the most recent year with the earliest diurnal location of those locations where spotted owl pairs were found before 31 July. Using these criteria, we distributed locations by years as follows: 2 in 1991, 12 in 1992, 4 in 1993, 15 in 1994, and 18 in 1995 (Fig. 1). At least 1 fledgling was produced at 44 of 51 spotted owl sites during the study period. Nest locations were used for those 44 sites, and pair locations were used for the remaining 7 sites.

Variables and Data Analysis

For spotted owl and random sites, and for each spatial scale, we determined mean proportions of forest stands in 6 categories of stand age and 4 categories of basal area, and we determined the weighted sum of residual trees per hectare. The 6 categories of stand age were 0-5, 6-20, 21-40, 41-60, 61-80, and >80 years. Age classes were chosen because of the following biological and management considerations associated with each class: (1) the 0-5 age class was thought to have no benefit to spotted owls, (2) stands 6-20 years old contain the highest abundance of woodrats (Hamm 1995), (3) stands 21-40 years old maintain relatively high densities of woodrats (Hamm 1995) and probably have structural characteristics that allow spotted owls to maneuver for foraging, (4) stands 41-60 years old have structural attributes for nesting (Folliard 1993) and sustained negligible timber harvest, (5) stands 61-80 years old have excellent structural characteristics and were subject to timber harvest, and (6) stands

Table 1. Description of 4 basal area classes used in analyses of northern spotted owl habitat on Simpson Timber Company property in northern California, 1991-95. Data were taken from a 398-ha circle around random and spotted owl site centers.

Basal area category (m^2/ha)	Random sites						Owl sites					
	Trees/ha		Volume[a]		Age		Trees/ha		Volume[a]		Age	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
<23	69.2	72.6	3.2	4.8	28.1	14.3	60.7	37.9	4.1	5.0	29.6	13.9
23-45	225.1	111.2	14.1	12.2	46.6	23.8	192.3	114.6	15.7	10.1	48.1	21.9
46-69	352.7	134.6	16.9	10.5	44.8	16.7	309.0	128.6	20.6	11.4	49.8	17.3
>69	507.7	234.0	27.2	16.4	58.1	22.6	400.5	217.7	33.1	19.9	56.1	22.8

[a] In million board meters/ha

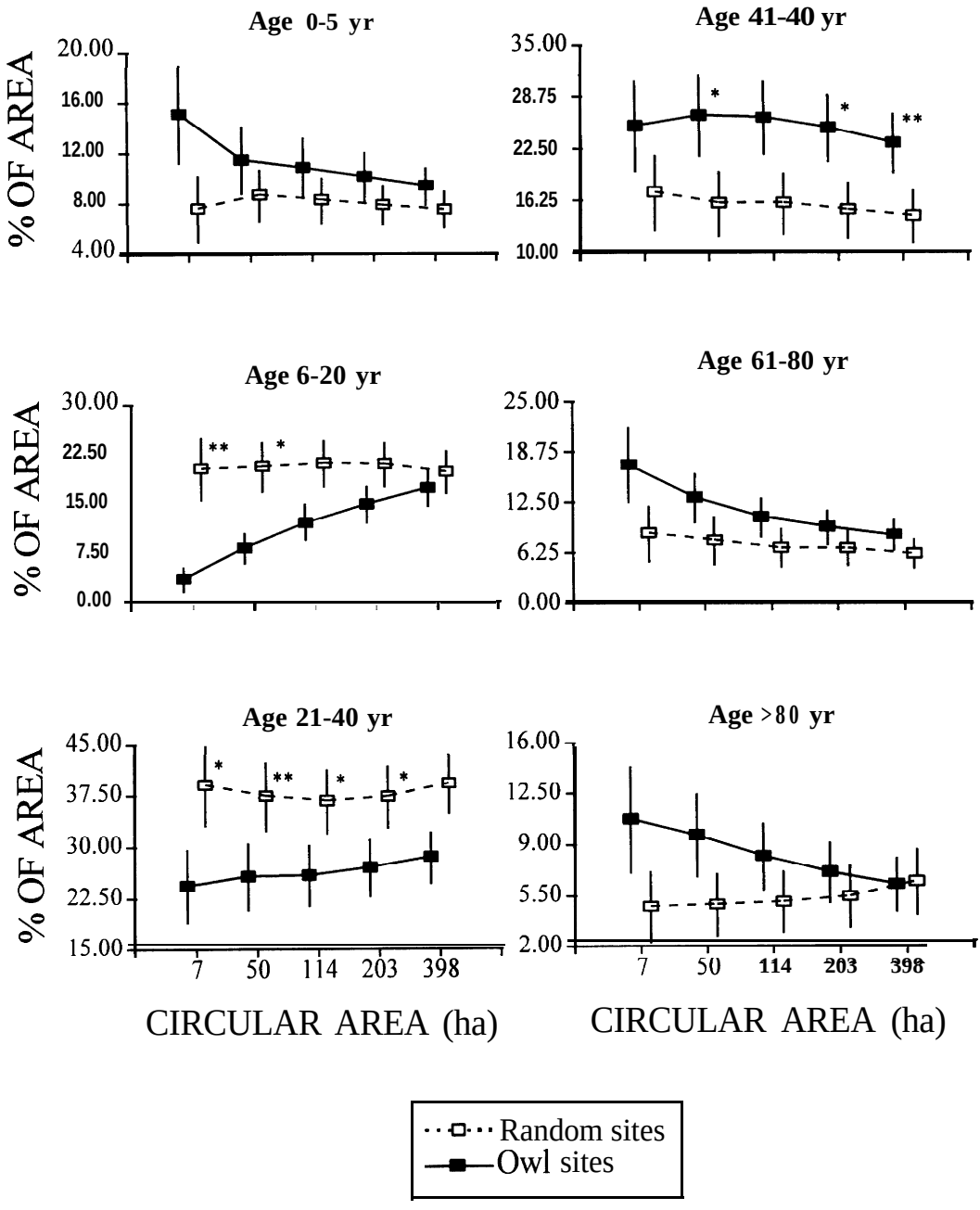

Fig. 3. Percentages of forest stand ages (X ± SE) from 5 circular scales centered on random (n = 51) and northern spotted owl (n = 51) locations. Study area was Simpson Timber Company property, northern California, 1991-95. P-values are for Mann-Whitney U-tests comparing random and spotted owl sites. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

>80 years old were few in number but could potentially contain trees with old-growth characteristics.

We created 4 discrete categories of basal area from a frequency distribution of basal area within the polygons of the largest spatial scale: <23, 23-45, 46-69, and >69 m2/ha (Table 1). All tree species were included in the basal area calculation. We calculated the proportion of a given circle that was composed of each of these

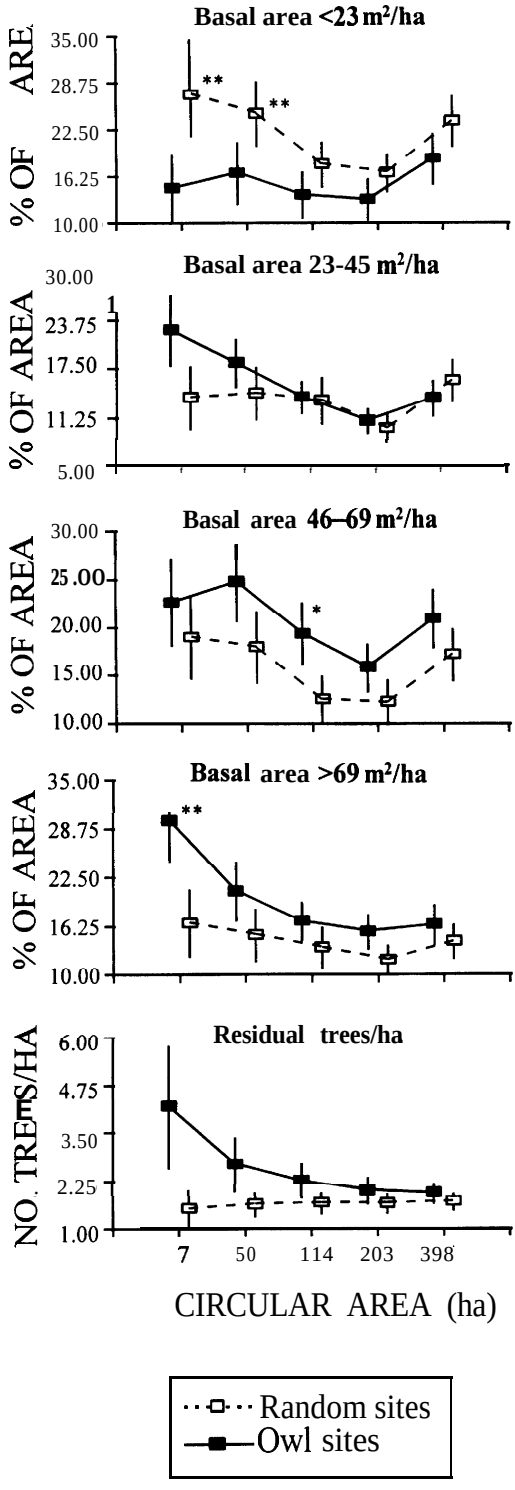

Fig. 4. Percentages of landscape attributes ($\bar{x} \pm$ SE) from 5 circular scales centered on random (n = 51) and northern spotted owl (n = 51) locations. Study area was Simpson Timber Company property, northern California, 1991-95. P-values are for Mann-Whitney U-tests comparing random and spotted owl sites. Residual trees/ha = number of weighted residual trees/ha. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

4 basal area classes. We used Pearson's correlation coefficients to evaluate correlations between basal area and age classes. All variables were used in the analysis, as the largest correlation was 0.53. To compare tree size in this study with that of other studies, we calculated the quadratic mean dbh as

$$\sqrt{(\text{basal area / no. trees}) \times (0.005454154)}.$$

Because of lack of normality, we used Mann-Whitney U-tests to (1) test the null hypothesis of no differences in habitat variables between spotted owl sites and random locations, and (2) test the null hypothesis of no differences in habitat variables between sites with low and high reproductive success. We used forward logistic regression (Hosmer and Lemeshow 1989) to (1) develop a model capable of predicting a spotted owl site; and (2) develop a model capable of predicting a site conducive to high reproductive success, given the above habitat variables. We used the Wald chi-square statistic to determine the significance of each individual variable's contribution to the model, and Hosmer and Lemeshow's (1989) goodness-of-fit statistic, $\hat{C}$, to determine the fit of the entire model (Loftsgaarden and Andrews 1992). To calculate $\hat{C}$, predicted probabilities of the logistic equations from the random-owl models were aggregated via the lo-percentile grouping method, where 10 groups were created, each with 10% of the sequential predicted probabilities. To increase cell sizes for the reproductive success models, we used 7 groups (13.7 percentile groupings) instead of 10. The goodness-of-fit statistic, $\hat{C}$, is designed to detect lack-of-fit. Thus, when $\hat{C}$ resulted in $P \leq 0.05$, the model was considered a poor fit and was rejected. These tests were performed at all spatial scales.

We measured reproductive success as mean yearly success; that is, the percentage of years that ≥ 1 young was successfully fledged (e.g., 1 of 5 yr = 20%). We calculated reproductive success based on the number of years that fledgling data were acquired. We had 5 years of data for 29 sites, 4 years for 17 sites, and 3 years for 5 sites. Preliminarily, we used linear regression to examine the relation between each independent variable and mean yearly success. We found the

Table 2. Significant coefficients fitted by logistic regression for northern spotted owls on Simpson Timber Company property, northern California, 1991-95. Models were attempted at 5 spatial scales (7, 50, 114, 203, and 398 ha) to distinguish spotted owl (n = 51) from random (n = 51) locations.

Scale Variable	Parameter estimate	SE	Wald χ^2	P-value	% classification	$\hat{C}$	P-value
50 ha					63.73	2.548	0.959
Intercept	1.012	0.358	8.014	0.005			
6-20 yr	-0.036	0.012	9.761	0.002			
21-40 yr	-0.016	0.006	6.414	0.011			
114 ha					61.76	6.505	0.591
Intercept	1.027	0.388	7.025	0.008			
6-20 yr	-0.03	0.011	7.222	0.007			
21-40 yr	-0.017	0.007	6.106	0.013			

predictive qualities of the independent variables to be poor (the highest r^2 for any given variable was 0.11); hence, we pursued more generalized tests, seeking differences in fecundity that were not detected at a predictive capacity but may have been present at a more coarse level (e.g., high-low differences instead of trend correlations). Yearly success was separated into 2 sets of categories to establish a binomial low-high success variable. We first split reproductive success into upper and lower 50th percentiles, and then into upper 25th and lower 75th percentiles (where the distribution of yearly success showed breaks; Fig. 2). The latter set was chosen to identify spotted owl habitats that facilitated reproductive success well above the remaining habitats.

We used SAS (SAS Institute 1988) for logistic regression, and NCSS (Hintze 1995) for Mann-Whitney U-tests. For all statistical analysis, significance was considered $P \leq 0.05$.

RESULTS

Landscape Patterns Around Spotted Owl Versus Random Locations

Spotted owl and random locations differed for 5 of 11 habitat variables at 3 of 5 spatial scales. There was more forest represented by age classes 6-20 years (at 7 ha: Z = -2.59, P = 0.009) and 21-40 years (at 50 ha: Z = -1.98, P = 0.047) in random than in spotted owl locations (Fig. 3) whereas spotted owl sites contained more of the 41-60-year age class (Z = 2.02, P = 0.043) than did random sites at 398 ha. Spotted owl sites did not differ from random locations in proportion of older forest (61-80 and >80 yr) or number of residual trees at any of the 5 spatial scales (Fig. 4). Trees in basal area class <23 m^2/ha were more abundant in random than in spotted owl sites (at 7 ha: Z = -2.27, P = 0.023; at 50 ha: Z = -2.12, P = 0.034), whereas trees in basal area

Table 3. Significant coefficients fitted by logistic regression for northern spotted owls on Simpson Timber Company property, northern California, 1991-95. Models were attempted at 5 spatial scales (7, 50, 114, 203, and 398 ha) to distinguish between sites with high (upper 25%; n = 13) and low (lower 75%; n = 38) reproductive success using percentage of years ≥1 owlet fledged.

Scale Variable	Parameter estimate	SE	Wald χ^2	P-value	% classification	$\hat{C}$	P-value
50 ha					74.51	4.436	0.488
Intercept	−1.531	0.408	14.040	<0.001			
Residual trees[a]	0.149	0.184	4.001	0.045			
114 ha					76.47	2.789	0.732
Intercept	−1.599	0.437	13.351	<0.001			
Residual trees	0.20 1	0.248	4.012	0.045			
398 ha					76.47	5.057	0.409
Intercept	−1.761	0.480	13.444	<0.001			
BA[b] 23-45 m^2/ha	0.044	0.020	4.538	0.033			

[a] Weighted sum of residual trees/ha.
[b] HA = basal area.

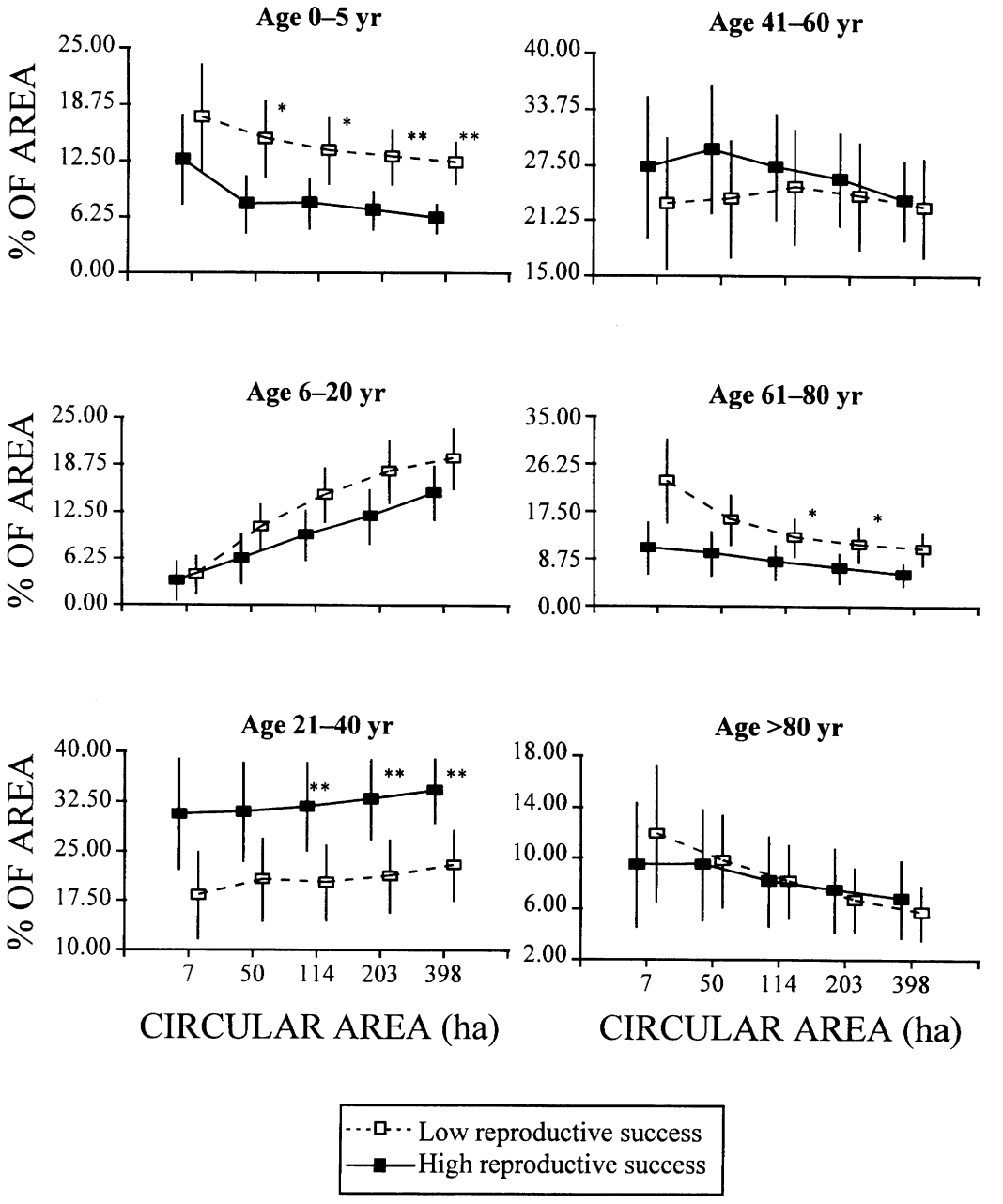

Fig. 5. Percentages of forest stand ages ($\bar{x} \pm$ SE) from 5 circular scales centered on northern spotted owl sites with high (upper 50th percentile; $n = 25$) and low reproductive success (lower 50th percentile; $n = 26$). Reproduction was measured as the proportion of years ≥1 owlet fledged on Simpson Timber Company property, northern California, 1991–95. *P*-values are for Mann-Whitney *U*-tests comparing spotted owl sites with high and low reproductive success. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

class >69 m²/ha were more numerous in spotted owl than in random sites (at 7 ha: $Z = 1.98$, $P = 0.047$; Fig. 4). Forward logistic regression found 2 landscape attributes at 2 spatial scales that distinguished ($P \leq 0.01$) spotted owl from random locations (Table 2). Proportions of 6–20 and 21–40-year-old stands were negative predictors of spotted owl habitat at the 50-ha and 114-ha circle sizes. The highest probability of the occurrence of habitat (70%) was projected when both 6–20 and 21–40-year-old age classes constituted 0% of the landscape.

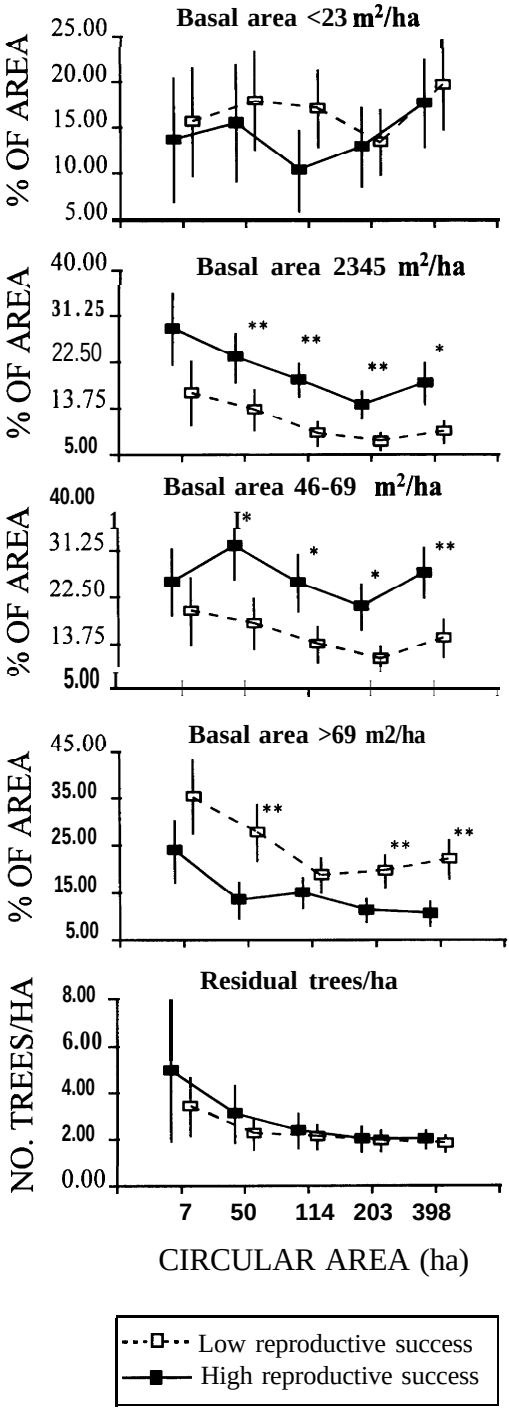

Fig. 6. Percentages of landscape attributes (X ± SE) from 5 circular scales centered on northern spotted owl sites with high (upper 50th percentile; n = 25) and low reproductive success (lower 50th percentile; n = 26). Reproduction was measured as the proportion of years ≥1 owlet fledged on Simpson Timber Company property, northern California, 1991-95. P-values are for Mann-Whitney U-tests comparing spotted owl sites with high and low reproductive success. Residual trees/ha = number of weighted residual trees/ha. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

Yearly Reproductive Success (Upper and Lower 50th Percentiles)

Sites with low reproductive success (lower 50%; n = 26) fledged ≥1 young in 0-33% of all years, whereas sites with high success (upper 50%; n = 25) fledged ≥1 young in 40-80% of all years (Fig. 2). Recent clearcuts (0-5 yr old) occurred in higher proportions at sites with low yearly success at 203 ha (Z = -2.09, P = 0.036) and 398 ha (Z = -2.41, P = 0.016). Sites with high yearly success contained higher proportions of 21-40-year-old stands at the 3 largest scales (at 114 ha: Z = 1.98, P = 0.047; at 203 ha: Z = 1.97, P = 0.049; at 398 ha: Z = 2.01, P = 0.045; Fig. 5). Sites with high and low success differed in 3 basal area classes: 23-45 (at 50 ha: Z = 1.94, P = 0.052; at 114 ha: Z = 2.60, P = 0.009; at 203 ha: Z = 2.28, P = 0.022), 46-69 (at 398 ha: Z = 2.08, P = 0.037), and >69 m²/ha (at 50 ha: Z = -2.14, P = 0.033; at 203 ha: Z = -1.93, P = 0.053; at 398 ha: Z = -2.49, P = 0.013).

The 2 smaller classes were found in greater amounts at sites with higher yearly success, whereas the largest class was found in higher amounts at sites with lower yearly success (Fig. 6). Forward logistic regression failed to model this representation of reproductive success via any of the independent variables.

Yearly Reproductive Success (Upper 25th Percentile, Lower 75th Percentile)

Sites with low reproductive success (lower 75%; n = 38) fledged ≥1 young in 0-40% of all years, whereas sites with high success (upper 25%; n = 13) fledged ≥1 young in 50-80% of all years (Fig. 2). Only 3 habitat variables distinguished sites in the upper quartile: they had significantly less of age class 61-80 years at all spatial scales (at 7 ha: Z = -2.08, P = 0.037; at 50 ha: Z = -2.30, P = 0.021; at 114 ha: Z = -2.59, P = 0.009; at 203 ha: Z = -2.64, P = 0.008; at 398 ha: Z = -2.306, P = 0.021; Fig. 7), more of basal area 23-45 m²/ha at the 203-ha size (Z = 2.11, P = 0.034), and more residual trees at 50 ha (Z = 2.03, P = 0.042) and 114 ha (Z = 1.94, P = 0.052; Fig. 8).

Two variables at 3 different spatial scales were fitted in the logistic models (Table 3). At

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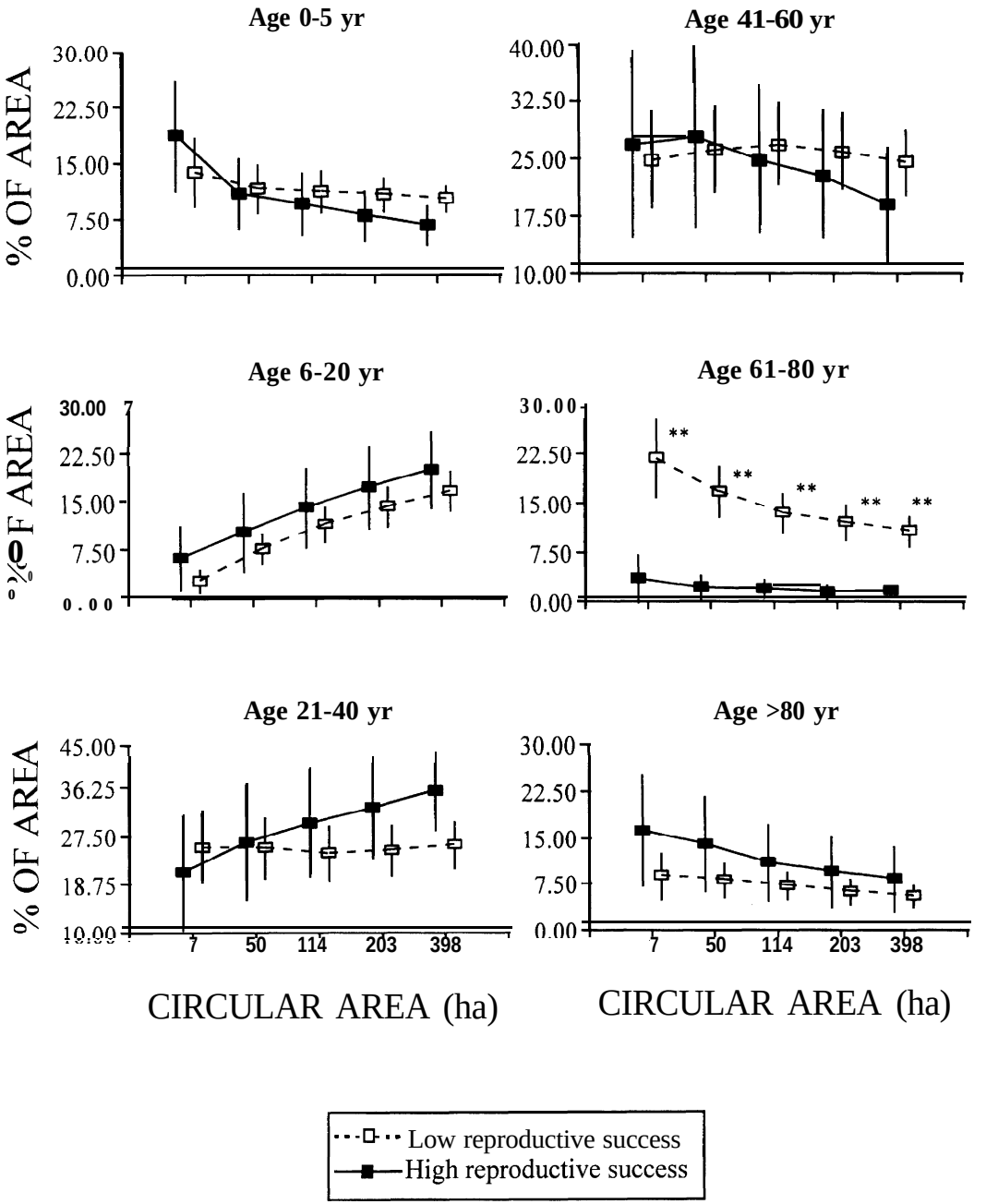

Fig. 7. Percentages of forest stand ages ($\bar{x} \pm$ SE) from 5 circular scales centered on spotted owl sites with high (upper 25th percentile; $n = 13$) and low reproductive success (lower 75th percentile; $n = 38$). Reproduction was measured as the proportion of years ≥1 owlet fledged on Simpson Timber Company property, northern California, 1991–95. P-values are for Mann-Whitney U-tests comparing spotted owl sites with high and low reproductive success. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

398 ha, proportion of basal area 23-45 m^2/ha was a significant positive predictor ($P = 0.033$) and at 50 and 114 ha, residual trees per hectare was a significant positive predictor of high yearly success ($P < 0.05$). When basal area of 23-45 m^2/ha composed 100% of the 398-ha circle, the model predicted a 93.3% probability of high yearly success (Fig. 9). For models using residual trees as the predictor, 22.2 trees/ha were required for a 95% probability of high yearly

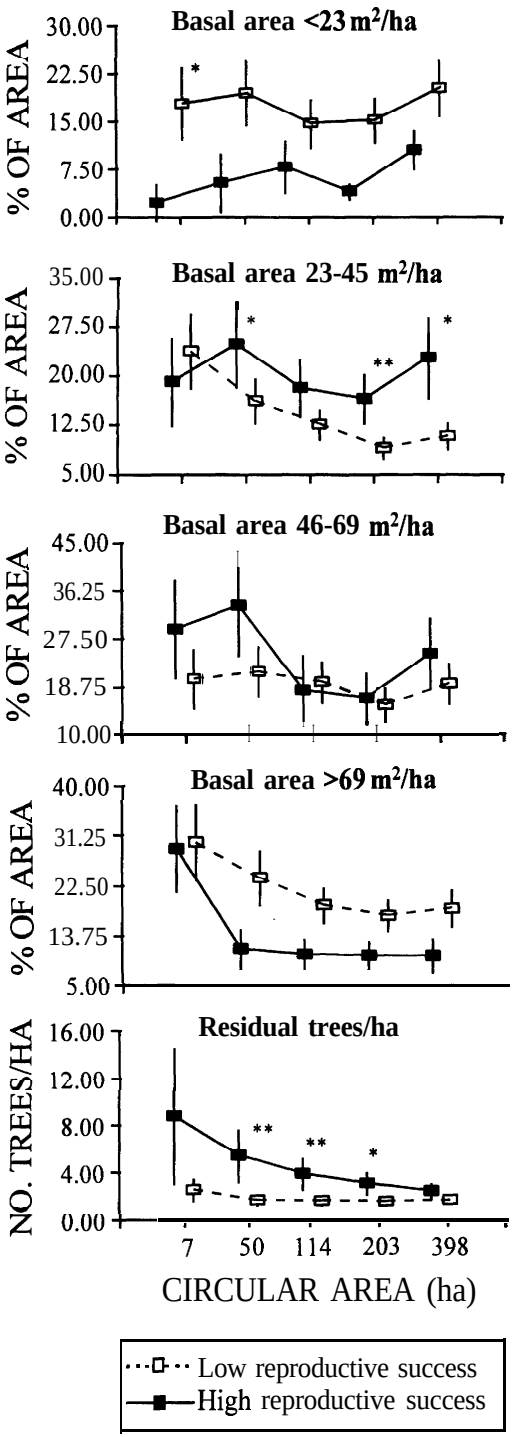

Fig. 8. Percentages of landscape attributes (X ± SE) from 5 circular scales centered on sites with high (upper 25th percentile; n = 13) and low reproductive success (lower 75th percentile; n = 38). Reproduction was measured as the proportion of years ≥1 owlet fledged on Simpson Timber Company property, northern California, 1991-95. P-values are for Mann-Whitney U-tests comparing spotted owl sites with high and low reproductive success. Residual trees/ha = number of weighted residual trees/ha. $^{**}P \leq 0.05$, $^{*}P \leq 0.10$.

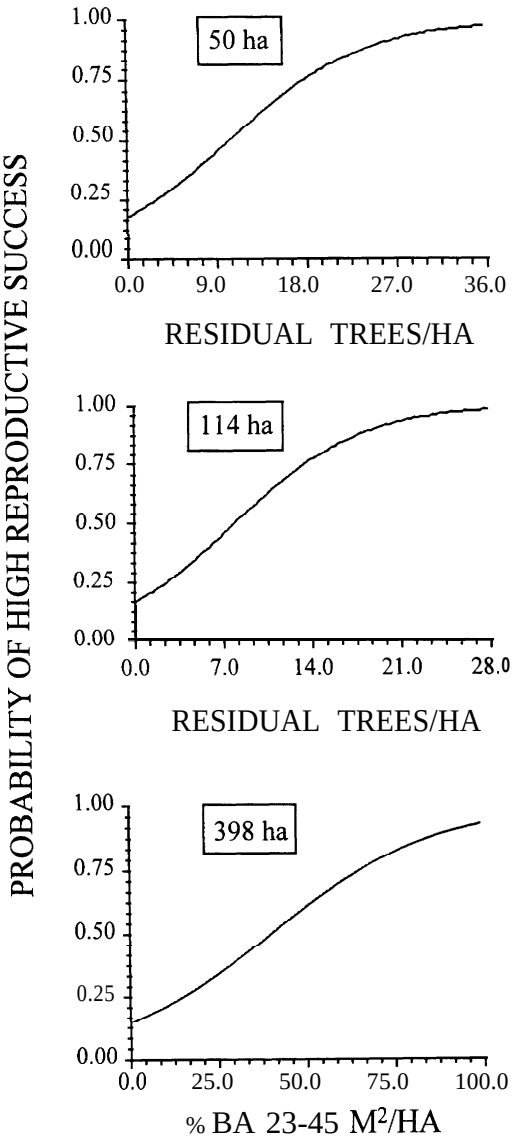

Fig. 9. Relation between northern spotted owl reproductive success and 2 habitat variables: mean proportion of basal area (BA) class 23-45 m²/ha, and residual trees (weighted sum trees/ha). The functions were created from logistic regression of landscape variables at 5 circular scales around 13 sites with high (upper 25%) and 38 sites with low (lower 75%) reproductive success on Simpson Timber Company property, northern California, 1991-95. Reproduction was measured as the proportion of years ≥1 owlet fledged.

success at 114 ha; at 50 ha, 30.0 residual trees/ha were required for a 95% probability of high yearly success.

DISCUSSION

Comparisons Between Random and Spotted Owl Sites

We found that spotted owls on STC's young-growth timberlands were positively associated with stands characterized by middle-aged and larger trees and negatively associated with stands that were younger and composed of smaller trees. We expected stands with basal area <23 m^2/ha to be less abundant at spotted owl sites than at random sites. These were young stands consisting of few stems with little volume (Table 1). Spotted owls probably cannot maneuver through young, brush-filled stands and may choose habitat containing less of this habitat type.

Although STC property contains negligible proportions of old-growth stands (>200 yr), spotted owl sites contained significantly higher proportions of stands with the greatest basal area (>69 m^2/ha) compared to random sites at 7 ha. LaHaye et al. (1997) found that California spotted owl nesting habitat had greater mean conifer basal area (37.1 m^2/ha) than did habitat at random points. However, a direct comparison is not possible because LaHaye et al. (1997) did not report proportions of basal area categories. Our observation that spotted owls were located in stands with the largest basal area on STC's landscape is consistent with other studies that have related spotted owl home ranges, nesting sites, and foraging locations with larger trees (Carey et al. 1992, Gutiérrez et al. 1992, Hunter et al. 1995). Larger trees provide increased structure for nesting and may also provide increased opportunities for finding thermally acceptable roosting and nesting locations (Barrows 1981, Verner et al. 1992). Although we found spotted owls at sites with the largest basal area class, these trees were not characteristic of trees in late seral stage forests (>53 cm dbh) and were smaller than trees reported in other studies (e.g., Solis and Gutiérrez 1990, Bart and Forsman 1992, Buchanan et al. 1993).

In northwestern California, Blakesley et al. (1992) found spotted owl roost and nest sites in stands of small timber (27.9-53.2 cm dbh) in proportion to their availability and hypothesized that spotted owls did not discriminate against small timber because these naturally occurring stands had a diverse species composition and a complex structure. Blakesley et al. (1992) further suggested this result may not be applicable to small timber regenerated after timber harvesting. In our study, trees within the basal area class >69 m^2/ha on STC property could be defined as small timber (37.87 $\pm$ 13.00 dbh; $\bar{x} \pm$ SD), and these stands regenerated following timber harvesting. We suggest spotted owls were using these stands because stands had a diverse species composition and complex structure. Based on observations by STC foresters, this structure was primarily the result of a diverse group of hardwood species (e.g., tanoak, madrone, California bay, black oak, big-leaf maple) that were a large component of most stands throughout the region. There is also strong evidence to suggest that because spotted owls are heat intolerant, a cooler summer climate may partially account for spotted owl use of these coastal forest stands (T. F. Ting, Humboldt State University, unpublished data). A direct comparison between forests on our study area and those on Blakesley et al.'s (1992) may be inappropriate because of different species composition and climatic regimes of the 2 study areas.

Spotted owls on STC lands appear to occupy stands of younger and smaller trees than those in other study areas. Without old-growth available, spotted owls lived in surroundings with higher proportions of stands 41-60 years old. The presence of spotted owls in young forest stands concurs with Folliard (1993), who found that 53% of spotted owl nests on STC lands were in stands 46-60 years old during 1990-91. Age classes 6-20 and 21-40 years occurred in significantly lower proportions at owl sites, suggesting these 2 age classes had poor structure (smaller limbs, lower canopy) for spotted owls. At spotted owl sites, percentages of stands 6-20 years old increased as spatial scale increased, while random sites maintained level proportions for all 5 spatial scales (Fig. 3). This positive relation between spatial scale and proportion of stands 6-20 years old suggests spotted owls choose core nesting locations lacking this young component.

Factors Influencing Reproduction

Although spotted owl locations were characterized by lower proportions of 21-40-year-old stands compared to random locations, spotted

owls at sites with higher proportions of 21–40-year-old stands had higher reproductive success (Fig, 5). Moreover, sites with high reproductive success contained lower proportions of the largest basal area class (using the 50th percentile stratification; Fig. 6) and the 61-80-year age class (using the 25-75th percentile stratification; Fig. 7). An explanation for this initially perplexing result may be in the prey base. Sakai and Noon (1993) found that woodrat abundance in Douglas-fir-tanoak forests of northern California was higher in sapling-poletimber seral stages (15-40 yr old) than in any other seral stages. Similarly, Hamm (1995) found woodrats in STC's rapidly growing coastal forests were most abundant in seedling-shrub (5-9 yr; 31.8 ± 6.5 woodrats/ha; $\bar{x}$ ± SE) and sapling-poletimber (10-20 yr; 31.3 ± 6.8 woodrats/ha) seral stages. Carey et al. (1992) suggested spotted owls may be drawn to areas of high woodrat concentrations and, in southwest Oregon, spotted owls selectively used young forest units, especially when woodrats were present (Carey and Peeler 1995). If woodrats are more abundant in the sapling-poletimber seral stage and spotted owls selectively use forest stands containing woodrats, then spotted owls with increased reproductive success would be expected to occupy sites containing more sapling-poletimber forest. However, spotted owls likely cannot forage or maneuver in such young forests (Rosenberg and Anthony 1992, Zabel et al. 1993). Thus, spotted owls would be expected to forage in stands that are young enough to contain an abundance of woodrats, yet old enough to have sufficiently high canopy to allow maneuverability. We suggest 21-40-year-old forest stands on STC lands have such characteristics, and stands at this age class may have the highest availability of woodrats. We also suggest basal area classes 23-45 and 46-69 m^2/ha were significantly more abundant at sites with high reproductive success because of high woodrat availability in these stands.

Reproductive rate is positively related to prey abundance in many species of owls, including barn owls *(Tyto alba;* Otenni et al. I972), great homed owls (*Bubo virginianus;* Houston 1975, Adamcik et al. 1978), northern hawk owls (*Surnia ulula;* Mikkola 1983), and tawny owls *(Strix aluco;* Petty 1987). Proportions of large mammalian prey and biomass were significantly greater in the diets of breeding pairs than nonbreeding pairs of spotted owls in California (Thrailkill and Bias 1989), and large mammalian prey were more frequent in the diet of breeding spotted owls once the young began to be fed (Barrows 1987). White (1996) determined that spotted owls eating woodrats fledged more young. This association could be an important factor to spotted owl reproduction on STC lands, as woodrats begin to use stands over 5 years old on STC property (Hamm 1995). Woodrats also may influence spotted owl reproduction because they were the most frequent component (46.5%) and the prey item with the highest biomass (69.8%) in the diet of spotted owls for this study area from 1989-90 (STC, unpublished data). Woodrats were also the most frequent prey item in a nearby study area (Zabe1 et al. 1995).

At the 50- and 114-ha spatial scales, there were more residual trees per hectare at sites with high yearly reproductive success (25-75 percentiles). These results support Thomas et al.'s (1990) suggestion that structural components such as large trees, snags, and logs left behind from early disturbances allowed for earlier use of regenerating stands by spotted owls. Residual trees also may provide the structural component that promotes high reproductive success for spotted owls in an environment lacking older components. The logistic regression models predicted that, at 114 ha, 22 residual trees/ha were needed for a 95% probability of high reproductive success; at 50 ha, 30 residual trees/ha were needed for a 95% probability of high reproductive success. The inverse relation between number of residual trees and spatial scale indicates a higher density of residual trees is important in habitat closer to the core of the spotted owl site (see Fig. 4).

MANAGEMENT IMPLICATIONS

We preface these recommendations by emphasizing that results obtained from this study apply only to north-coastal California forests managed with clearcut silvicultural practices. Furthermore, these recommendations are primarily intended for use on commercial timberlands where growing harvestable trees is the principal land-use objective.

Our data showed that high reproductive success of spotted owls on STC lands was associated with stands characterized by 21-40-year-old trees and stands with basal area of 23-45 and 46-69 m^2/ha. We hypothesize that these associations were a result of high prey availability

in those stands. Clearcuts were associated with low reproduction at the 2 largest spatial scales (203 and 398 ha). Hence, to minimize the effect of harvest on reproduction, clearcuts would need to be restricted to at least 1.1 km beyond nests.

We found that residual trees (larger trees left from past logging operations) provided clear benefit to spotted owl reproduction. The positive association of high reproductive success with residual trees was at relatively small scales (50 and 114 ha), indicating they were most important when located near the core of the nest site. If large blocks of young stands with a high residual tree component could be retained, then habitat conducive to high reproductive success would be created. Given the current age at which stands are harvested (approx 60 yr), these stands would be available for spotted owl use for about 20-40 years before harvesting activities (resulting in clearcuts) would disrupt spotted owl reproduction.

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