SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER FIVE

Habitat Associations

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1 INTRODUCTION

Habitat for Spotted Owls includes characteristics of vegetation, climate, geography, prey, predators, competitors, and interactions between these factors. Prey, predators and competitors of Spotted Owl are covered in other chapters of this report. This chapter focuses on the vegetational, climatic, and geographic aspects of Spotted Owl habitat. Research has emphasized vegetation composition of Spotted Owl habitat, at least in part because timber harvest and other management activities that affect vegetation can be modified by humans, whereas climate and geography cannot. The emphasis in this chapter on forest and landscape attributes reflects the historic research emphasis. Within sections of this chapter, findings are generally organized by geographic province (see figure in introductory chapter), from north to south and west to east. Few studies of habitat use by juvenile Northern Spotted Owls have occurred since 1990, and all studies of owls that did not use radio-telemetry were conducted in March-August. Consequently, unless otherwise noted, habitat associations discussed in this chapter apply to territorial Spotted Owls during spring and summer.

More studies of habitat relationships have been conducted on the Spotted Owl than any other raptor in the world (Lõhmus 2003). Habitat use by Northern Spotted Owls has been evaluated by a variety of methods and at several spatial scales for more than two decades (Gutiérrez et al. 1995; Franklin and Gutiérrez 2002). In general, studies completed by 1990 showed that Northern Spotted Owls consistently used old-growth forests, forests of mixed mature and old-growth, or, especially in the Redwood region, mature forest with structural characteristics similar to old-growth stands, for foraging, roosting and nesting in proportions greater than expected based on availability. Thomas et al. (1990:164) characterized Northern Spotted Owl habitat as follows:

> “Structural components that distinguish superior Spotted Owl habitat from less suitable habitat in Washington, Oregon, and northwestern California include: a multilayered, multispecies canopy dominated by large (>30 inches in d.b.h.) conifer overstory trees, and an understory of shade-tolerant conifers or hardwoods; a moderate to high (60 to 80%) canopy closure; substantial decadence in the form of large, live coniferous trees with deformities—such as cavities, broken tops, and dwarf mistletoe infections; numerous large snags; ground-cover characterized by large accumulations of logs and other woody debris; and a canopy that is open enough to allow owls to fly within and beneath it.”

Johnson (1980) provided a framework for discussing orders of habitat selection: first-order selection is the physical or geographical range of a species, second-order selection determines the home range of an individual, third-order selection involves the use of habitat components within the home range, and fourth –order selection is choice of, for example, prey items within an individual habitat component. In this hierarchy, higher orders of selection are conditional upon lower orders. For example, selection of forest stand types by a Spotted Owl within its home range is constrained by selection of the home range. Following Johnson’s (1980) framework, research reviewed in this section examined second- and third- order selection.

Establishing the spatial extent of an owl's home range and relative use within the home range (second-order selection) requires use of radio-telemetry. In several studies, composition of owl home ranges or core areas established using radio-telemetry was compared to composition of a larger forested landscape. Because the intensity and high cost of radio-telemetry studies limited sample sizes, many recent landscape level studies on Spotted Owls have approximated home range or core area composition (second-order selection) using Geographic Information technology and extensive Spotted Owl location data collected during demographic studies and other owl surveys. In these studies, circles centered on Spotted Owl nest or roost locations were drawn on vegetation maps to approximate home range or core areas. Corresponding circles were located randomly within forested landscapes, and comparisons were then made between the composition and, sometimes, spatial configuration of habitat (including fragmentation) with owl sites. Recently, several studies have modeled demographic responses of owls (survival, recruitment, and reproductive rates) as a function of habitat available to owls.

Third-order selection by Spotted Owls has been evaluated at a variety of spatial scales, from gross categorization of forest stands to detailed measurements of forest structure. Stand condition is a general classification based on species composition, tree age or size, canopy closure, fire regime, soil, climate and/or topographic characteristics. Researchers have defined stand conditions differently among studies, but, in general, an effort was made to distinguish stands characterized by large, old trees from those characterized by smaller-sized, younger trees. Alternatively, several studies classified stands according to physiognomic stages of stand development (Buchanan et al 1995:302, after Oliver 1981):

> "The stand initiation stage is the establishment of the regenerating stand by an even-aged cohort of trees and may last > 40 years. During stem exclusion, the second stage, the initial cohort occupies all available growing space and prevents other trees from invading the stand. This is followed by the understory reinitiation stage, where shade-tolerant (or moisture-limited) tree species begin to develop ≥ one strata in the understory. Forests of the old-growth stage are characterized by uneven-aged cohorts that result from perturbations of various scale and intensity."

At a finer spatial scale, forest structure (canopy cover, tree diameter distribution, snag density, coarse woody debris, etc.) was quantified from detailed measurements at nest, roost, and random locations. At this scale, most studies measured habitat association by comparing characteristics of areas used by owls with areas available within the home range, within the same stand, or at random locations.

In the following, we review what we have learned about Northern Spotted Owl habitat associations since 1990. In particular, we ask which aspects of our previous understanding are confirmed by recent research and which aspects have changed or clarified. We pay particular attention to similarities and differences in findings among provinces.

2 HOME RANGES AND CORE AREAS

2.1 HOME RANGE AND CORE AREA SIZE

Home range sizes of Northern Spotted Owls have been estimated on five study areas in Washington, Oregon and California since 1990 (Table 5.1). Home range sizes were estimated by fitting owls with backpack or tail-mounted radio transmitters, determining owl locations by triangulation on the radio signal, and calculating the area traversed by the owls based on the distribution of the triangulated owl locations. The simplest and most consistently applied analytical method for calculating Spotted Owl home range size was to estimate the Minimum Convex Polygon (MCP), the area of the smallest polygon containing all of an owl's radio locations. The MCP may include portions of a landscape not used by an owl, and therefore may be more appropriately considered the area traversed rather than the area used by an owl (Carey et al. 1992). Other methods of estimating home range size include calculation of MCP using a subset (e.g. 95%) of the spatial extent of locations (95% MCP), modified minimum convex polygon (MMCP) or various smoothing methods, including kernel estimators. Kernel estimators use probabilistic models to estimate the relative use of areas traveled by an animal. A utilization distribution, which is a probability density function that indicates the likelihood of an animal occurring at each point within the range, quantifies relative use. Home range size is then reported typically as the area containing that portion of the utilization distribution where the animal is likely to be found 95% of the time (Kernohan et al. 2001). Kernel estimates are less sensitive to sample size and outliers than MCP estimates (Kernohan et al. 2001).

Home range area for Northern Spotted Owl pairs varied by physiographic province and forest type and among individual owls within a study area (Table 5.1). MCP home range estimates reported from 1990 to present were similar to those tabulated by Thomas et al. (1990:194).

A home range core area was defined as the area within a home range that receives disproportionately high use (Bingham and Noon 1997), and may be estimated empirically using kernel methods. Core area sizes were extremely variable among owls but similar at two study areas in the Oregon Coast Range, averaging 94 ha (SE = 14.9; n = 24; range = 5 to 273) even though MCP home range size (more sensitive to sample size; see above) differed by study area (Glenn et al. 2004).

The influence of landscape attributes on home range size has been inferred by comparing differences in forest age, amounts of mature and old-growth forest, forest fragmentation, tree species composition and distribution of major prey species with differences in home range area. Carey et al. (1992) found that the area traversed by owls (100% MCP home range) was 85% larger in more heavily fragmented Douglas fir forest in the Oregon Coast Range and 237% larger in more heavily fragmented mixed conifer forest in the Klamath Province relative to less fragmented areas of the same forest types/geographical areas (Table 5.1). However, the amount of old forest within home ranges was similar among study areas in the Carey et al. (1992) study.

Glenn et al. (2004) compared home range sizes in two study areas in the Oregon Coast Range. The Elliot State Forest study area (ESF) contained a mix of old, mature and pole size conifer, and the North Coast Range study area (NCR) contained mostly forest < 80 yrs old. Both study areas consisted of approximately 23-25% hardwood forest, predominantly in riparian areas. Home ranges were larger at NCR than ESF whereas core area size was similar among study areas (Table 5.1). Variation in home range size was best explained by models containing the proportion of mature/old forest within the home range (41% of variation explained), with smaller home ranges having greater proportions of mature/old conifer forest. There was very little mature/old forest at NCR. On average, owl locations at both study areas were closer to edges between hardwood forest and other cover types and farther from forest-nonforest edges than random points, but the authors noted this was not true for all individuals.

In contrast to these findings, in study areas dominated by late-successional forest in the southern Oregon Coast Range and California Klamath Province, home range size of Spotted Owls was not correlated with the proportion of the home range in old-growth forest (Zabel et al. 1995). Rather, the proportion of the diet containing woodrats explained 41% of the variation in Spotted Owl home range size. Home ranges were smaller where woodrats dominated the diet ($r^2 = 0.64$, $n = 15$) and larger where flying squirrels dominated ($r^2 = 0.56$, $n = 15$). Within one study area where woodrat density was estimated, home range size was negatively correlated with woodrat abundance ($r^2 = 0.41$, $n = 12$; Zabel et al. 1995).

The response of one Spotted Owl to timber harvest was evaluated in a detailed study in the Oregon Coast Range (NCR study area, above; Meiman et al. 2003). This male owl's breeding season home range and core area sizes were similar pre- and post-harvest but its nonbreeding season home range and core area sizes were larger after harvest. The owl's core area of use shifted away from the thinned stand following harvest. Inferences from this study were limited because it included only one individual owl.

2.2 HOME RANGE AND CORE AREA COMPOSITION

Many researchers have compared stand conditions surrounding owl locations to random locations by mapping circles of various radii around owl nests or roosts, and then comparing forest conditions within the circles. In nearly all cases, the amount of mature and old-growth forest was greater within circles containing owls than random locations, ranging from 30–78% at owl sites and 6-63% at random sites (Table 5.2; see also Swindle et al. 1999).

One study in the Eastern Cascades of Washington found results contrary to this general trend (*Irwin et al. in press*). *Irwin et al.* (*in press*) found more mature and old-growth forest (> 64 cm dbh) in random locations than owl locations and more forest 20-64 cm dbh in owl locations than random locations. Furthermore, owl locations were positively associated with proximity to riparian habitat and negatively associated with trees 13-19 cm dbh and with elevation. *Irwin et al.* (*in press*) hypothesized that development of dense understories of shade tolerant trees 13-19 cm dbh, which resulted from fire suppression since 1910, may have led to abandonment of 45 owl territories in mesic forests of their study area.

Within commercial forest in the California Redwood Zone, 200 ha circles centered on owl nests contained forest > 60 yrs old in similar proportion to that found within 200 ha circles centered randomly on forest not used for nesting (nest circles mean = 42%, SE = 6%; random circles mean = 41%, SE = 6%; Folliard et al. 2000). However, the area at nest sites composed of forest

31-45 yrs old (mean = 46%, SE = 8%) and 45-60 yrs old (mean = 55%, SE = 8%) was greater than unused sites (31-45 yr old forest mean = 29%, SE = 6%; 45-60 yr old forest mean = 34%, SE = 7%), whereas the area of forest 8-30 yrs old was lower at nest than unused sites (nest site mean = 24%, SE = 5%; unused site mean = 53%, SE = 9%; Folliard et al. 2000).

In a study area (BLM Arcata Resource Area [ARA]) characterized by small, isolated patches of old growth forest surrounded by areas of extensive timber harvest in the California Klamath Province, Gutiérrez et al. (1998) compared landscape composition within 200 ha plots surrounding Spotted Owl nest and roost sites (n = 29) with landscape locations unused by Spotted Owls (n = 15). Owl use sites contained 32% mature and old-growth forest (SE = 4) compared to 22% at unused sites (SE = 3). Habitat dominated by brush (< 25% canopy cover, woody plants < 15.2 cm dbh) comprised 24% of owl use areas (SE = 1) and 40% of unused areas (SE = 18). Cover type heterogeneity, measured by Simpson's heterogeneity index, was lower at used than unused areas (used = 0.60, SE = 0.02; unused = 0.65, SE = 0.03). Landscape characteristics of owl use sites in the ARA were also compared to an equal number of owl use sites in another study dominated by larger more contiguous areas of old forest (the Willow Creek Study area [WCSA] of Franklin et al. 2000 and Hunter et al. 1995). The WCSA owl sites contained more mature and old-growth forest (WCSA mean = 50%, SE = 3), more pole and medium conifer (WCSA mean = 14%, SE = 1%; ARA mean = 7%, SE = 2%), and less brush (WCSA mean = 10%, SE = 2%) than ARA.

In some studies, landscape composition was evaluated within nested circles. In general, differences between owl locations and random sites diminished as circle size increased (Hunter et al. 1995, Ripple et al. 1997, Meyer et al. 1998, Swindle et al. 1999, *Perkins 2000*). Amount of mature and old-growth forest was higher in owl sites than random landscape locations even within annuli created by concentric circles up to 3.4 km radius in one study in Oregon (Meyer et al. 1998) and up to 0.6 km radius in another study in Oregon (Swindle et al. 1999). Differences in outer rings indicated that differences between larger circles were not simply artifacts of differences in nested smaller circles in this population (Meyer et al. 1998).

In general, across studies, hardwood and younger conifer forest types were not greater within owl circles than random circles with the following exception: greater amounts of hardwood forest were found in owl than random sites beyond the smallest (0.8 km radius) circles in the Klamath Province of Oregon (Meyer et al. 1998).

In the Oregon Coast Range Spotted Owls were negatively associated with 0-40 and 41-70 yr old stands at three of four spatial scales evaluated (50, 100, and 600 ha), positively associated with 101-200 yr old stands at 200 ha scale and positively associated with > 200 yr old stands at all scales based on stepwise logistic regression for 82 owl and 82 random sites (*Zabel et al. 2001*).

2.3 REPRODUCTION, RECRUITMENT AND ADULT MORTALITY

Hicks et al. (2003) measured productivity, subadult recruitment and adult turnover rates at 100 Spotted Owl sites spanning the Washington Cascade Range over a 10 yr period. Owl nest sites were grouped into five vegetation zones, from west to east: western hemlock, silver fir, interior western hemlock, grand fir, and interior Douglas fir. Physical and geographic parameters (precipitation, elevation and longitude) were weakly correlated only with productivity (regressions $P > 0.05$ and $r^2 < 0.05$). The number of young fledged per territory differed by vegetation zone, decreasing from east to west. Three young were fledged in 15% of nesting attempts in the Interior Douglas fir (easternmost) zone, 3% of attempts in the grand fir zone, and never in the three westernmost zones. Owls in the three westernmost zones had lower adult turnover rates and lower subadult recruitment rates than owls in the two easternmost zones. Because this study was not based on mark-recapture methods, turnover and recruitment were confounded with detectability. However, trends found in this study were confirmed by estimates of survival and fecundity in a meta-analysis using mark-recapture data (see Demography Chapter).

Irwin et al. (*in press*) compared Spotted Owl reproductive rates among Fire Management Analysis Zones (FMAZ), which were based on vegetation associations, natural fire regimes, and other factors (see section 4.2). Similar to the findings of Hicks et al. (2003), the highest Spotted Owl reproductive rates were in Ponderosa pine/Douglas fir forests and grand fir mixed coniferous forest, and the lowest reproductive rates were in western hemlock and subalpine forests of the Eastern Cascades, Washington. *Irwin et al.* (*in press*) also compared reproductive output of Spotted Owls inside Late-Successional Reserves (LSR) with owls outside LSRs. Assignment of an owl to inside or outside and LSR was based on whether the majority of a 200 ha circle surrounding the owl site center was comprised of LSR or not. Mean productivity was 0.60 young/yr (SE = 0.04) in LSRs and 0.72 young/yr (SE = 0.06) outside LSRs. *Irwin et al.* (*in press*) did not present the location of LSRs among FMAZ in their study; therefore we can not evaluate the degree to which differences in owl productivity among FMAZ and between LSR/non-LSR may be confounded.

An index to Spotted Owl reproductive rates in the Klamath Province, Oregon, increased with increasing proportion of mature and old-growth forest in the landscape around nest sites (Ripple et al. 1997). The reproductive index standardized the number of young fledged at a site to the average number of young fledged in the same years, to account for missing data from some sites in some years, given the annual variation in the number of young fledged throughout the study area (Ripple et al. 1997).

Within commercial forest in the California Redwood Zone, Spotted Owl sites with the highest reproductive success (n = 25) had greater proportions of 21-40 year-old stands within a 398 ha circle surrounding the site center than sites with lower reproductive success (n = 26). Reproductive success was measured as the proportion of years when ≥ 1 juvenile owl fledged. However, Spotted Owl site centers had lower proportions of 21-40 year-old stands than random locations (Thome et al. 1999). Thome et al. (1999) hypothesized that Spotted Owls may have benefited from higher woodrat availability in the 21-40 year-old stands. Thome et al. (2000) also found for the same Spotted Owl sites that those with at least one turnover in four annual intervals (n = 30) had lower proportions of 21-40 year-old stands (mean = 0.23, SE = 0.05) than those without turnovers (n = 21, mean 21-40 year- old stands = 0.36, SE = 0.06). Fifty percent of the new recruits were subadults (1 or 2 years old). Because female Spotted Owls generally do not breed until at least 3 years old (see Demography chapter), turnover rates and reproductive rates were confounded in this study.

Neither *Irwin et al.* (*in press*), Ripple et al. (1997), nor Thome et al. (1999) measured survival rates in relation to the same independent variables with which they measured reproductive rates, so it is unknown whether the factors positively associated with owl reproduction were also positively associated with owl survival.

2.4 FOREST FRAGMENTATION AND LANDSCAPE CONFIGURATION

Franklin and Gutiérrez (2002) conducted a meta-analysis of the effects of forest fragmentation and heterogeneity on all three subspecies of Spotted Owls. In this meta-analysis, Northern Spotted Owls were represented by seven studies in the Olympic Peninsula, Washington, Coast Range, Klamath Province, Eastern and Western Cascades of Oregon, and Klamath Province of California (Lehmkuhl & Raphael 1993, Ripple et al. 1991, *Johnson 1992*, Meyer et al. 1998, Ripple et al. 1997, Hunter et al. 1995, *Morganti 1993*). Meta-analysis confirmed that sites occupied by Northern Spotted Owls contained greater amounts of mature and old forest than randomly located sites in forested landscapes (see section 2.2; Table 5.2). Comparisons of fragmentation and heterogeneity were limited because dissimilar metrics were used in individual studies. However, six metrics were common to two to three studies, and the following three showed consistent relationships to owl occupancy across studies: mean patch area of mature and old-growth forest, amount of patch interior of mature and old-growth forest, and a fragmentation index (GISfrag of Ripple et al. 1991). Magnitude of effects for these three metrics were similar between the Western Cascades and Klamath Provinces, which suggested that owl site occupancy was positively associated with old forest patch area and size of patch interior and negatively associated with the fragmentation index.

Other measures of fragmentation varied between owl and random sites for individual study areas. On the Olympic Peninsula, in addition to greater amount of owl habitat and larger mean patch area, owl sites (n = 78) had lower patch density and isolation indices than random sites (n = 100; Lehmkuhl and Raphael 1993). Within 3258 ha circles, percent owl habitat was 46% for owl sites and 34% for random locations. Nest patches were larger than the largest old conifer patches in random circles in the Klamath Province, Oregon (Ripple et al. 1997).

Subsequent to the meta-analysis of Franklin and Gutiérrez (2002), *Perkins* (*2000*) found Simpson's Evenness Index was higher within 112 ha surrounding nest than random non-nest locations, indicating a more even distribution of cover types around nest than non-nest locations in the Oregon Coast Range. Additionally, percent old growth and young stands with remnant large-diameter trees were greater around nest locations and discriminated between nest and non-nest locations. *Perkins* (*2000*) also found differences between old growth stands used for nesting and old growth stands not used for nesting were best explained by the ratio of core:edge of the stand and complexity of the stand shape, both of which were higher at nest stands than non-nest stands.

In the California Redwood Zone, 200 ha circles centered on owl nests (n = 60) contained more edge (juxtaposition of different cover types or age class of the same cover type) and were lower on slopes than 200 ha circles centered randomly on forest not used for nesting (n = 60; Folliard et al. 2000). Dispersing juvenile owls in the Coast Range, Klamath Province and Western Cascades, Oregon, showed no differences in use of forests with low, medium, or high levels of fragmentation, based on the numerical value of a fragmentation index calculated within 1.6 km radius circles (Miller et al. 1997).

Keithley and Motroni (*2000*) compared vegetation composition and configuration within 200 ha circles among > 300 Spotted Owl sites (exact number not specified) and 55 randomly selected non-owl sites throughout the northern Coastal province in California. Vegetation was classified as: "preferred owl habitat" (conifer stands with ≥ 61 cm quadratic mean diameter [qmd] and ≥ 70% canopy cover, and hardwood stands with ≥ 76 cm qmd and ≥ 70% canopy cover); "marginal habitat" (conifer stands with ≥ 61 cm qmd and < 70% canopy cover, conifer stands with < 61 cm qmd, hardwood stands with ≥ 76 cm qmd and < 70% canopy cover, and hardwood stands with < 76 cm qmd); "woodrat habitat" (conifer stands with < 61 cm qmd and 10-50% canopy cover and hardwood stands with < 76 cm qmd and 10-50% canopy cover); grass and shrub; non-forest (urban, barren and water). Spotted Owl sites were further classified according to land management (private, public managed, public reserve). Spotted owl sites of all three land management categories contained more preferred owl habitat, more marginal habitat, more woodrat habitat and a higher mean Shape Index (Shape Index increases as patch shapes become more irregular) than non-owl sites (ANOVA multiple means test $P < 0.05$). Mean fractal dimension, perimeter to area ration and Shannon Evenness Index were similar among Spotted Owl sites and non-owl sites (*Keithley and Motroni 2000*).

Zabel et al. (2003) built models to predict Spotted Owl site occupancy in the Klamath Province in California. They found that models which included habitat edge and core area variables as well as non-linear relationships between occupancy and roosting and foraging habitat performed better (based on correct classification of independent data sets) than models based only on linear relationships to roosting and foraging habitat. Among 200, 550 and 900 ha scales, models performed best at 200 ha, although the authors note that this may be due to a larger sample size for the smaller scale.

Zabel and Pagliughi (*2003*) tested the model of Zabel et al. (2003) on portions of the Six Rivers and Mendocino National Forests and found that the model performed poorly in predicting Spotted Owl presence and absence; only 48% of points were correctly classified. Failure of the model to perform well was likely due, at least in part, to the fact that habitat data used in the model were from 200 ha buffers around call point locations rather than owl roost or nest locations.

2.5 SURVIVAL, REPRODUCTION AND SITE OCCUPANCY IN RELATION TO FOREST FRAGMENTATION AND LANDSCAPE CONFIGURATION

Ripple et al. (1997) found that an index to reproductive rates (see above) at 20 owl sites in the Klamath Province, Oregon, increased with increasing proportion of old conifer forest in the landscape ($r = 0.64$, $P = 0.03$). Old conifer forest included open (40 to 59%) and closed (≥ 60%) canopy stands dominated by conifers ≥ 50 cm dbh.

Thrailkill et al. (*1998*) modeled territory occupancy, nest success and turnover on individual owl territories (n = 64) as a function of the amounts of various habitat types within circles of five different radii (1.1–3.4 km). Territory occupancy and nest success were negatively related to the amount of clearcut area surrounding owl site centers across spatial scales. Turnover rate was negatively related to the amount of suitable habitat within the smallest circles and positively related to the amount of clearcut area within 1.6 and 1.9 km radius circles.

Meyer et al. (1998) examined reproductive success as a function of landscape characteristics, including fragmentation, at 50 Spotted Owl sites in the Oregon Coast Range, Klamath Province, and Western Cascades. Reproduction was not related to any landscape measures in the Coast Range nor Cascades, but in the Klamath Province was positively correlated with increased fractal dimension, increased number of old-growth patches, and increased amount of hardwood forest within 2.4-km-radius circles centered on owl nests (or centers of activity if no nest was known; adjusted $R^2 = 0.56$).

Four studies modeled the effects of weather variables and landscape characteristics on temporal and spatial variation of Northern Spotted Owl survival and reproductive rates (Franklin et al. 2000, *Olson et al. 2004*, *Anthony et al. 2002a, Anthony et al. 2002b*). Methods are described in the Demography chapter (section 2.1), as are analyses pertaining to weather (section 2.2). The following results pertaining to habitat are a reiteration of those in the Demography chapter (section 2.1). Franklin et al. (2000) and *Olson et al.* (*2004*) also estimated habitat fitness potential (λ_H) of individual owl sites using modified Leslie projection matrix methods. Habitat fitness potential was interpreted as follows: $\lambda_H = 1$ indicates that owls in a territory are replacing themselves, $\lambda_H < 1$ indicates that owls in a territory are not replacing themselves, and $\lambda_H > 1$ indicates that owls in a territory are more than replacing themselves.

In the California Klamath Province, survival was positively and non-linearly associated with the amount of interior older forest (> 100 m from an edge), the amount of edge between older forest and other vegetation types, and showed a quadratic (convex) relationship to the distance between patches of older forest (Franklin et al. 2000). Reproductive output was negatively and non-linearly associated with the amount of interior older forest, had a quadratic (concave) relationship to the number of older forest patches, and was positively associated with the amount of edge between older forest and other vegetation types. Thus, there appeared to be a trade-off between the benefits to survival conferred by interior older forest and benefits to reproduction conferred by less interior older forest and more convoluted edge between the two habitat categories. Estimates of λ_H ranged from 0.438 to 1.178. Based on 95% confidences intervals, 69% of owl territories had estimates of $\lambda_H > 1$, indicating owls at these territories more than replaced themselves. Franklin et al. (2000) suggested that habitat quality may determine the magnitude of λ (population trend) and recruitment may determine variation around λ. In addition, owls in territories of higher habitat quality (i.e., $\lambda_H > 1$) had greater survival during inclement weather than those in poorer quality habitat.

In the central Oregon Coast Range, survival had a quadratic (convex) relationship to the amount of mid- and late-seral forest within 1500 m of owl site centers (707 ha circles; *Olson et al. 2004*). The best model explained only 16% of the variation in the data. Of the variation explained by the model, habitat accounted for 85%. Reproductive output was positively related to the amount of edge between mid- and late-seral forests and other habitat classes. The best model explained 84% of the total variability; however, the habitat variable accounted for only 3% of the variation explained by the model. A mixture of older forests with younger forests and nonforested areas appeared to benefit owl life history traits. Estimates of λ_H ranged from 0.74 to 1.15 (mean = 1.05, variance = 0.005), with 95% confidence intervals around λ_H for all but one territory overlapping 1, indicating a potentially stationery population based on habitat pattern (*Olson et al. 2004*).

In the western Cascades, owl survival had a quadratic (concave) relationship to the amount of non-habitat within 1500 m of owl site centers. The best model of survival explained 58% of total variance, and habitat accounted for 32% of the variance explained by the model. Owl productivity showed a negative linear relationship to the largest patch size of old conifer (> 50 cm dbh) forest within 1500 m of owl site centers (*Anthony et al. 2002a*). The best model explained 77% of the variation in owl productivity; however, 99.6% of this variation was accounted for by owl age, 0.4% by weather, and a negligible amount by habitat.

In the southern Cascades, two nested circles (167 and 1565 ha) and the ring between the circles (1388 ha) were used to characterize habitat at owl sites (*Anthony et al. 2002b*). The best model of owl survival indicated that survival increased non-linearly with the amount of mature and old growth forest within 167 ha around site centers and had a quadratic (convex) relationship to the amount of non-habitat in the 1388 ha ring. These two habitat covariates explained 54% of the spatial variation in survival; temporal variation was essentially zero (*Anthony et al. 2002b*). Owl productivity was positively related to the proportion of mature and old-growth forest within 600 m of owl site centers. However, the best model accounted for 25% of the total variance in reproductive output and the habitat variable only accounted for 7% of the model variance. Seventy-four percent of the model variance was explained by a biannual pattern in reproduction ("even-odd year effect") and the experience of male owls on a territory (*Anthony et al. 2002b*).

2.6 FIRE EFFECTS

In 1994, the Hatchery Complex wildfires burned 17,603 ha in the Wenatchee National Forest, eastern Cascades, Washington, affecting activity centers of six Northern Spotted Owl sites (*Gaines et al. 1997*). Spotted Owl habitat within 2.9 km radii of the activity centers was reduced by 8–45% (mean 31%) due to direct effects of the fire and by (cumulatively) 10-85% (mean = 55%) due to delayed mortality of fire-damaged trees and insect caused tree mortality. Spotted Owl habitat was defined as having ≥ 60% canopy closure, numerous snags, and ≥ 2 canopy layers, and was measured from field-verified aerial photo interpretation before the fire, immediately post-fire, and one year post-fire (*Gaines et al. 1997*). Spotted Owl habitat loss was greater on mid-upper slopes (especially south-facing) than within riparian areas or on benches (*Gaines et al. 1997*). Direct mortality of Spotted Owls was assumed to have occurred at one site. Data were too sparse for reliable comparisons of site occupancy or reproductive output between sites affected by the fires and other sites on the Wenatchee National Forest.

Two wildfires burned in the Yakama Indian Reservation, eastern Cascades, Washington, in 1994, affecting home ranges of two radio-tagged Spotted Owls (*King et al. 1997*). Although the amount of home ranges burned was not quantified, owls were observed using areas that received low and medium intensity burning. No direct mortality of Spotted Owls was observed even though thick smoke covered several owl site centers for a week.

2.7 SUMMARY OF HOME RANGES AND CORE AREAS

Home range size of Spotted Owls appeared to be influenced by a variety of factors, including proportion of mature and old growth forest within the home range, forest fragmentation, and dominant prey species. Despite variation in methods used, all studies outside the Eastern Cascades and Redwood zone showed that Spotted Owl core areas contained greater proportions of mature/old forest than random or non-use areas. In the Eastern Cascades, this trend was reversed; further research should examine putative causes of these regional differences and whether the differences in use of mature/old forest are related to regional differences in population trend (see Demography chapter).

Studies consistently showed that mature/old forest patch area was an important predictor of forest occupancy by Spotted Owls. While a fragmentation index was negatively associated with site occupancy in some studies, a trade-off between large patches of mature/old forest and juxtaposition of land cover types appeared to benefit Spotted Owls in other studies. We recommend that additional studies with long-term survival and reproductive data conduct analyses similar to those of Franklin et al. (2000) and *Olson et al.* (*2004*). Such studies may elucidate the geographical extent to which the trade-offs between interior patch area of mature/old forest and edge with other cover types occurs.

3 STAND CONDITION

3.1 JUVENILE DISPERSAL

Only one study after 1990 reported on habitat use by dispersing juvenile Northern Spotted Owls; it was conducted in the Oregon Coast Range, Klamath Province and Western Cascades (Miller et al. 1997). Old-growth and mature forest were combined in analyses and defined as forest dominated by trees > 53 cm dbh, generally 100% canopy closure, at least two height classes of trees, and decayed living trees, snags and downed woody material. Other cover types defined were closed sapling-pole-sawtimber stands (2.5 to 53 cm dbh and > 60% canopy closure), open sapling-pole stands (2.5 to 53 cm dbh and < 60% closure) and clearcuts. Used and available habitat were measured within 1.6 km radius circles surrounding owl locations. Dispersal was divided into two phases: transience and colonization. Transience was defined as "a period of extensive movement from one area to another" and colonization as "the period when an animal attempts to become established in a new area" (Miller et al. 1997:143). Available habitat was defined by the area with a 1.6 km radius of roosts because the mean straight-line dispersal distance of juvenile owls during the transience phase of dispersal was 1.6 km. Mature and old-growth forest was used slightly more than expected based on availability during the transience phase (n = 21 owls) and nearly twice its availability during the colonization phase (n = 18 owls). Closed pole-sapling-sawtimber habitat type was used roughly in proportion to availability in both phases; open sapling and clearcuts were used less than expected based on availability during colonization.

3.2 FORAGING AND ROOSTING

In all studies that used radio-telemetry to establish forest stand types used by Spotted Owls for foraging and roosting it was assumed that nighttime locations represented foraging behavior and daytime locations represented roosting behavior.

In the Western Cascades of Washington, Spotted Owls used mature/old forest (dominated by trees > 50 cm dbh with > 60% canopy closure) more often than expected for roosting during the non-breeding season (n = 175 roosts) and used young forest (trees 20-50 cm dbh with > 60% canopy closure) less often than expected based on availability (Herter et al. 2002).

In the Oregon Coast Range and Klamath Provinces, old-growth forest was the only forest type used for foraging and roosting in greater proportion than its availability at the landscape scale (Carey et al. 1992). At a finer scale, however, owls used portions of young forests for foraging in greater proportion than its availability, especially where woodrats were present (Carey and Peeler 1995). The latter analysis was based on frequency of use by owls within approximately 20 ha landscape units classified according to cover type and topography.

In the Western Cascades of Oregon, 23% of foraging locations (n = 38) obtained using radio telemetry were in late seral/old-growth stands (≥ 80 yrs old), even though these stands comprised only 10% random locations (n = 50; Irwin et al. 2000). Similarly, 13% of foraging locations and 38% of random locations were in stands <40 yrs old. Most of the study area was harvested 60 years previous to the study or regenerated after fires 100 yrs previously. Consequently, "nearly all stands sampled contained more than one large (> 80 cm dbh) tree/ha" and foraging stands had more large snags (> 50 cm dbh) than random stands (Irwin et al. 2000:179).

In Redwood National and State Parks, California, the use of old-growth stands for roosting (83% of roosts) was greater than expected based on availability (41% of random stands) and use of second-growth stands (6% of roosts) was less than expected based on availability (51% of random stands; n = 37 roosts, n = 37 random locations; *Tanner 1999*). Use of partially harvested stands (11% of roosts) was similar to random locations (8% of random stands; *Tanner 1999*).

3.3 NESTING

In mixed conifer forest of the Eastern Cascades, Washington, 27% of nest sites were in old-growth forests, 57% were in the understory reinitiation phase of stand development, and 17% were in the stem exclusion phase (Buchanan et al. 1995). Buchanan et al. (1995) did not evaluate the proportion of the greater landscape in the different stages of stand development. In a study of 20 nests in the Klamath Province, Oregon, all were found in old conifer forest (Ripple et al. 1997). In the Western Cascades, Oregon, 50% of Spotted Owl nests (n = 44) were in late seral/old-growth stands (≥ 80 yrs old) and none were found in stands < 40 yrs old although 10% and 38% of random locations (n = 50), respectively, were in these stand ages (Irwin et al. 2000; see section 3.2 for description of study area).

In commercial redwood forest of California, 54% of nests were found in stands 31-60 yrs old, 30% in stands 61-80 yrs old, 17% in stands > 80 yrs old (Folliard et al. 2000). Mean percent of these forest age classes in 60 sites centered randomly on forest not used for nesting were 31, 14, and 7%, respectively. Sixty-four percent of Spotted Owl pairs nested in stands with residual, older trees present.

3.4 SUMMARY OF STAND CONDITION

Spotted owls consistently used mature/old forest disproportionately for natal dispersal, foraging, roosting and nesting compared to other cover types available.

4 STAND STRUCTURE

4.1 FORAGING AND ROOSTING

Within Olympic National Park, Mills et al. (1993) compared nine characteristics of Spotted Owl roost or nest (n = 32) and non-response (n = 230) sites in old-growth forest. Variables measured were: community type, vertical canopy layering, cover of lowest canopy layer, number of trees > 80 cm dbh on a 0.1 ha plot, distance between trees, average snag dbh, distance between snags, percent cover of vascular plants, percent cover of logs. Stepwise logistic regression correctly classified 90% of stands on the western side of the park and 79% of stands on the eastern side. Only two of the variables measured were consistently important in regression models. Spotted owls tended to roost in stands with greater vertical canopy layering and greater snag diameter.

North et al. (1999) measured forest structural variables at Spotted Owl foraging locations obtained from radio-telemetry of 11 owls in the Olympic Peninsula and Western Cascades, Washington. Measurements were taken at four plots within each of 43 stands representing low (n = 13), medium (n = 12), and high use (n = 18) for foraging. Six stand attributes differed by and were positively related to owl use intensity: density of trees ≥ 80 cm dbh, snag basal area, snag volume, intact snag volume, foliage volume, and tree height class diversity.

Buchanan et al. (1999) used data from an intensive Spotted Owl study using radio-telemetry on the western Olympic Peninsula to choose 16 foraging and roosting locations that were not in old-growth habitat and 16 random locations from within MCP home ranges. They then separated roosting and foraging locations into those with single detections and those with multiple detections. They measured tree and snag density by diameter class, canopy cover, cover of downed wood, and shrubs within three 0.8-ha plots at each location. Locations with a single visit were similar to random locations whereas locations with multiple visits had greater snag density > 50 cm dbh and higher canopy closure. Buchanan et al. (1999) recommend that younger forests managed for Spotted Owls on the Western Olympic Peninsula should contain ≥ 10 snags/ ha that are > 50 cm dbh.

Vegetation structure was measured at Spotted Owl roosts (n = 146) located using radio-telemetry during the non-breeding season in the Western Cascades, Washington (Herter et al. 2002). Spotted owls roosted in areas lower in elevation, with larger tree dbh, fewer trees/ha, greater canopy cover, less shrub cover, and less down wood than found at random locations (n = 60).

Stepwise logistic regression selected the number of trees/ha, shrub cover, and volume of down wood for discriminating between roost and random stands.

King (*1993*) compared vegetation characteristics between 219 owl use sites (86% roosting locations combined with 14% foraging locations) and 209 random sites in the Eastern Cascades, Washington, on managed forest in the Yakama Indian Reservation. Nearly all stands in the study area had been selectively harvested prior to the study (uneven age management). Owls used sites with higher canopy closure, higher basal areas of medium-sized fir trees (27.5-52.4 cm dbh), higher slopes, taller mature-sized trees (52.5-89.9 cm dbh), and lower shrub height, grass cover, bare ground, and herb cover. Canopy cover was by far the most important discriminator between owl and random sites. *Pidgeon* (*1995*) conducted a study similar to that of *King* (*1993*) on the unmanaged portion of the Yakama Indian Reservation, comparing 163 owl use sites (88% roosting locations combined with 12% foraging locations) with 138 random loctations. Ground cover of litter, canopy cover, basal area of large conifers, and log volume were the best discriminators between used and random locations and were higher at random locations.

In Redwood National and State Parks, California, roost sites of Spotted Owls were at lower elevations, had more canopy layers, a higher density of old growth trees and more small woody debris (1-30 cm diameter) than random sites (n = 37 roosts, n = 37 random locations; *Tanner 1999*).

At the southern end of its range in Marin County, CA, roost sites of Northern Spotted Owls differed from random locations by having greater variation in tree diameters, greater number of potential nest trees, higher percent slope, and more large woody debris (*Chow 2001*). Potential nest trees were defined as trees with either a cavity > 48 cm along the tree axis, a broken top > 53 cm diameter with live branches over it, or an existing platform nest > 60 cm diameter.

Ting (*1998*) compared the ambient temperature at spotted owls roost locations with temperatures at random locations within the same stand and random locations within adjacent stands of younger forest on the Willow Creek Study Area (WCSA), Klamath Province, California. Temperatures at roosts were lower than at random sites in adjacent younger stands; temperatures at random locations within roost stands were intermediate between roost and younger stand locations. *Ting* (*1998*) also compared temperature profiles within mature/old growth and younger forest at both WCSA and Redwood National Park (RNP) in coastal California. Both age classes of forest stands were similar in RNP and were cooler than stands on the WCSA. Mature/old growth stands were cooler than younger stands at WCSA.

4.2 NESTING

Hershey et al. (1998) compared stand structure of nest sites (n = 105) and paired random sites in four Provinces (Olympic Peninsula, Washington, and Coast Range, Klamath and Western Cascades, Oregon). Random sites were restricted to stands dominated by trees > 50 cm dbh. Evidence of fire was present at 86% of nest sites and 76% of random sites. The total density and basal area of live trees were higher at nest than random sites, mostly due to greater densities and basal area of trees < 23 cm dbh. Variation in tree diameters between nest and random sites was similar. Density and basal area of broken-top trees and volume of down logs in decay classes 4 & 5 (most decadent) were higher at nest than random sites.

On the eastern slope of the Cascades, Washington, on the Wenatchee National Forest, Buchanan et al. (1995) compared habitat characteristics at 62 nest sites with those at 62 paired random sites within the same forest stands. Nests were in mixed conifer forests within grand fir, Douglas fir and western hemlock forest associations. Nest sites had lower canopies of dominant/codominant and intermediate trees, more Douglas fir trees 35-60 cm dbh, more ponderosa pine trees 61-84 cm dbh, greater live tree basal area, greater basal area of decadent snags, and less basal area of more intact snags. Volume of coarse woody debris and percent canopy closure were similar between nest sites and random sites within nest stands. Evidence of past fire was visible at 92% of nest sites. These data were reanalyzed by Buchanan and Irwin (1998) by stratifying nests within five Fire Management Analysis Zones (FMAZ). FMAZ were designated by the Wenatchee National Forest based on vegetation associations, topography, precipitation, frequency of lightning strikes, and estimates of fuel loading and fire frequency. In addition to differences in tree species among zones, trees were smaller and younger and had higher canopy closure in more xeric zones.

Buchanan (*1996*) also characterized vegetation around spotted owl nests in the Klickitat region of the eastern slope of the Cascades, Washington. In contrast to the study on the Wenatchee National Forest to the north (Buchanan et al. 1995; previous paragraph), terrain in the Klickitat region was less steep and > 50% of the 31 nest sites examined had experienced partial logging, primarily by pre-commercial thinning (*Buchanan 1996*). Nest trees in the Klickitat region were larger and older than trees in the Wenatchee National Forest, but occurred in stands dominated by younger trees (*Buchanan 1996*). Evidence of past fire was visible at 71% of nest sites. *Buchanan* (*1996*) found few structural differences between nest sites and paired random sites within the same stands (e.g., total basal area and height of live trees, total canopy closure, snag density, volume of downed wood) except that the number of canopy layers was greater at nest plots (median = 2.0) than random plots (median = 1.8; $z = 2.20$, $P = 0.028$). Total basal area of live trees and number of canopy layers were greater at sites on federal than non-federal (state and private) lands.

In the Oregon Coast Range, density of snags < 53 cm dbh, number of horizontal vegetation layers and density of broad-leaved trees were higher at Spotted Owl nest ($n = 51$) than random ($n = 50$) sites whereas density of live conifers 53–86 cm dbh and density of snags 53–86 cm dbh were lower at nest than random sites (*Thrailkill et al. 1998*). Random sites were located in stand types used by Spotted Owls for nesting within the study area (*Thrailkill et al. 1998*).

Irwin et al. (2000) compared vegetation structure among nesting ($n = 44$), foraging ($n = 38$) and random ($n = 50$) stands within home ranges of 12 pairs of Spotted Owls in the Western Cascades, Oregon. Random sites were restricted to habitat types used by owls. Stands sampled for foraging were all from owl pairs that nested at least once and received disproportionate use (4% of telemetry locations in 1% of adaptive kernel home range; all were within 60% adaptive kernel core area). Zero nests, 13% of foraging and 38% of random locations were in stands < 40 yrs old. Foraging and nesting stands had significantly greater number of large (> 50 cm dbh) snags than random stands. Volume of large and small woody debris was greater at foraging than nesting and random stands. Herbaceous and shrubby understory vegetation < 0.5 m tall was less at foraging than nesting and random locations for most stand age classes. All stands used by owls had canopy cover > 80% (estimated using a spherical densiometer).

Pious (*1994*) measured vegetation and physiographic characteristics in 52 nest and 22 roost stands in commercial forest of the California Coast Range (both Redwood and Douglas fir zones). Although no statistical comparisons were made and random sites were not measured, total canopy closure in nest and roost stands was similar (nest mean = 83%, SE = 1.7, median = 86; roost mean = 85%, SE = 1.0, median = 86). Mean conifer tree age was 73 years (SE = 12.0, median = 63, n = 41) in nest stands and 63 years (SE = 5.1, median = 69, n = 14) in roost stands.

LaHaye and Gutiérrez (1999) measured stand structure at 44 Spotted Owl nests and 44 paired random sites within the same stands in the Coast Range and Klamath Provinces of California. Among 17 variables compared, basal area of trees > 90 cm dbh, basal area of hardwoods 41-60 cm dbh, and basal area of Douglas-fir snags were different between nests and random points, and were greater at the nest site for all three variables.

On the Klamath National Forest, in the California Klamath and Cascade provinces, stand structure was measured at 29 Spotted Owl nests and 27 paired random sites within the same stands (*White 1996*). No differences were found in any variable measured (e.g., tree and snag basal area by diameter class, log volume, shrub cover, canopy cover, ground cover) except diameter of the tree at the plot centers.

On commercial timberlands in the California Klamath and Cascade provinces, stand structure was measured at 12 Spotted Owl nests, two nests immediately adjacent to the timberland, and two Spotted Owl roost sites (*Farber and Crans 2000*). Mean canopy closure within one ha plots was 67% (range 48–80) using a sighting tube. In other stands, mean canopy closure was 16 to 23% lower using a sighting tube than using densiometers (*Farber and Crans 2000*). Quadratic mean diameter of trees > 12 cm dbh within one ha surrounding nest trees averaged 31 cm (SE = 2). The number of large snags (> 28 cm dbh)/ha and pieces of large woody debris (> 28 cm diameter)/ha were highly variable among plots (mean = 32 snags, SE = 8; mean pieces of large woody debris = 181, SE = 18). These data were compared to data from 18 non-randomly selected commercially thinned stands. Mean canopy closure in thinned stands was 46% using a sighting tube. Quadratic mean diameter of trees > 12 cm dbh in thinned stands was 33 cm (SE = 1, range 23–42).

4.3 SUMMARY OF STAND STRUCTURE

Forest stand structural attributes positively associated with foraging, roosting and nesting included vertical canopy layering, tree height or diameter diversity, canopy volume, canopy closure, snag diameter, snag basal area or volume, tree diameter and log volume. These attributes correspond to those identified by Thomas et al. (1990) as important components of Northern Spotted Owl habitat. Notably, positive relationships were found with the aforementioned attributes whether the samples of owl and random locations were within old growth forest, non-old growth forest, National Parks, public land, private land, or an Indian Reservation. Even in the Eastern Cascades and Redwood zone, where owl core areas contained lower or equivalent proportion of old forest compared to random locations, large trees (often residuals older than the surrounding stand) were important components of Spotted Owl nest locations (Buchanan et al. 1995, *Irwin et al. in press*, *Lowell Diller, pers. comm.*).

5 NEST TREES

On the Olympic peninsula, tree species used for nesting included western hemlock, Douglas fir, western red cedar, Pacific silver fir, and grand fir (Forsman and Giese 1997). Seventy-eight percent of 116 nests were in live trees and 22% in snags. Fifty-three percent of nests were in side cavities (the most common nest type in the western side of the study area, at 71%), 37% were in top cavities (the most common nest type in the eastern side, at 51%) and 10% were in external platforms. The majority of top cavity nests in live trees were in trees with secondary tops growing above the cavity. On average, external platform nests were in smaller trees (mean dbh = 89 cm, SE = 15.7) than cavity nests (mean dbh = 142 cm, SE = 6.2). External platforms were in old stick nests built by common ravens or goshawks (n = 5), debris platforms on deformed limbs caused by dwarf mistletoe infections (n = 3) and debris accumulations at locations where trees had split into multiple tops (n = 3). The mean dbh of all nest trees was 137 cm (SE = 5.9, range = 30-379 cm), while the mean dbh of nest trees in the west was 158 cm (SE = 6.0), and in the east was 107 cm (SE = 6.3). Location of nests was similar to random locations in slope aspect and position on slope, but more nests than expected were on steeper slopes. Seventy-one percent of nests were in forests dominated by trees ≥ 100 cm dbh with multi-layered canopies; 19% were in forests dominated by trees 50-99 cm dbh with multi-layered canopies; 8% were in forests with a mosaic of small (13-49 cm dbh) and large (≥ 50 cm dbh) trees; 2% were in relatively even-aged forests of trees with dbh 50-99 cm.

Hershey et al. (1998) measured characteristics of 105 nest trees in four Provinces (Olympic Peninsula, Washington and Coast Range, Klamath and Western Cascades, Oregon). Eighty-eight percent of nest trees in Oregon were Douglas fir. In the Olympic Peninsula, nest trees were well distributed among Douglas fir, western hemlock and western red cedar. In the four provinces, 73-97% of nests were in live trees. Side cavities comprised 3-15% of nests in the Coast Range, Klamath, and Western Cascades and 67% of nests on the Olympic Peninsula. Top cavities made up 55-87% of nests in the Coast Range, Klamath and Western Cascades and 27% in the Olympic Peninsula. External platforms accounted for 41% of nests in the Klamath Province and 7% in the remaining three provinces. In the Klamath Province, more nests than random sites were on the lower third of slopes; in the other provinces, most nest and random sites were on the middle third of slopes. Mean dbh of all nest trees was 139 cm (SE = 5.2); dbh of trees with cavity nests (mean = 144 cm; SE = 5.6 cm) was greater than trees with platform nests (mean = 120 cm; SE = 15.4).

In the northern portion of the eastern Cascades, Washington, 92% of 85 nest trees were in Douglas fir (Buchanan et al. 1993). Use of Douglas fir trees was higher than expected based on tree species composition of nest stands. Eighty-eight percent of nest trees were live and 12% were snags. Eleven percent of nests were in side cavities, 6% in top cavities, 80% in external platforms, and 4% on live branches adjacent to the trunk. Among platform nests, 31% were on mistletoe brooms, 51% were in stick nests on top of mistletoe brooms, and 12% were stick nests. Stick nests were apparently made by goshawks. Median age of nest trees was 137 yr (range 66-

700). Nest tree age was greater than the age of randomly selected trees. Nest trees on south-facing slopes were older (median age 165 yr) and larger in diameter (dbh mean = 76, SE = 5) than those on north-facing slopes (median age 127, dbh mean = 58, SE = 3). Trees with external platform nests were smaller than those with top or side cavity nests. The disproportionate use of Douglas firs for nesting was attributed to the prevalence of mistletoe infections in this species (Buchanan et al. 1993). For this same data set, nest trees in xeric zones tended to be on north-facing slopes whereas nest trees were more evenly distributed among slope aspects in other zones (Buchanan and Irwin 1998).

In the southern portion of the eastern Cascades, Washington, 81% of 31 nest trees were in Douglas fir, 13% in ponderosa pine, 3% in Grand fir and 3% in black cottonwood (*Buchanan 1996*). Use of Douglas fir trees was higher than expected based on tree species composition of nest stands. Twenty-three percent of nests were in cavities, 65% in external platforms, and 13% on live branches. Among platform nests, 35% were on mistletoe brooms, 40% were in goshawk nests and 25% were on broken tops of trees. Median age of nest trees was 250 yr (range 66-980). Nest tree age was greater than the age of randomly selected trees (*Buchanan 1996*).

In the Eugene BLM District, Oregon Coast Range, 89% of 53 nest trees were in Douglas fir, 6% in western red cedar, 4% in bigleaf maple and 2% in western hemlock (*Thrailkill et al. 1998*). Eighty percent of nests were in living trees with broken tops, usually with secondary live tops. Mean nest tree dbh was 146 cm (range 93-213; *Thrailkill et al. 1998*).

In commercial forestland in the Western Cascades, Oregon, 65% of nest trees (n = 44) were >120 years old and 73% were > 80 cm dbh; these trees were legacies from previous stands subjected to either timber harvest or fire (see above; Irwin et al. 2000). Seventeen nests were in cavities, 22 in external platforms, and five were unknown. Nest trees in young/mid-seral (< 80 yrs old) stands were often much older than majority of trees in the stand (Irwin et al. 2000).

Two studies described nest trees on commercial forest in the California Coast Range. In forest owned by Louisiana-Pacific Corporation, nests (n = 97) occurred in redwood (73%), Douglas fir (14%), tanoak (8%), grand fir (3%), western hemlock (1%) and golden chinquapin (1%; *Pious 1994*). Sixteen percent of nests were in side cavities, 14% in top cavities and 65% were in stick platforms. Mean nest tree dbh = 106 cm (SE = 69, range 26-378; *Pious 1994*). On Simpson Timber Company Land, 53% of 60 Spotted Owl nests were in tree deformities (broken tops, platforms, or cavities) and 47% of nests were external platforms (mostly squirrel or vole nests; Folliard et al. 2000). Seventy-three percent of nest trees were residual trees (older than the surrounding stand).

Three studies described nest trees in National and State Parks and other reserved land of the California Coastal province. Eleven nests were found in Humboldt and Del Norte Counties; 10 nests were in redwood trees and one was in a Douglas fir; three were in cavities and eight were in external platforms (*Tanner 1999*). Mean dbh of nest trees was 257 cm. In Marin County, among 28 Spotted Owl nests in redwood, Bishop pine, hardwood, Douglas fir, and mixed forest types, 89% were in conifers (Douglas fir, redwood and Bishop pine) and 11% in hardwoods (California bay and tanoak; *Chow 2001*). Only one nest (4% of total) was in a side cavity, 25% of nests were in top cavities, and 71% were in external platforms. Mean conifer nest tree dbh was 113 cm while mean hardwood nest tree dbh was 48 cm. In another study in Marin County, 42% of 120 nests were in redwoods, 38% in Douglas fir, 8% in bishop pine, 7% in California bay, 3% in tanoak, and 2% in coast live oak (*Fehring et al. 2003*). Among the 120 nest trees, those containing platform nests (88%) were smaller in diameter (mean = 92 cm; SE = 42) than those containing cavity nests (12%; mean = 126 cm; SE = 54; P = 0.001; *Fehring et al. 2003*).

Of 69 nests in the California Coast Range and Klamath Provinces measured by LaHaye and Gutiérrez (1999), 83% were in Douglas fir, 9% in redwood, and < 2% each in Bishop pine, tan oak, canyon live oak, black oak, chinquapin, and white fir. Twenty percent of nests were in side cavities, 60% in top cavities, and 20% in platforms. Nest tree dbh was similar among trees containing different nest types (side cavity mean was 157 cm, SE = 3 while top cavity mean was 138 cm, SE = 1, and platform mean was 119 cm, SE = 3).

On the Klamath National Forest, in the California Klamath and Cascade provinces, 41% of 29 nests were in cavities and 59% on platforms, with cavity nests occurring predominantly in Douglas fir forest and platform nests found mainly in mixed conifer forest (*White 1996*). Differences in nest type used were attributed to past timber harvest; however, timber harvest was confounded with forest type (mixed conifer forests had been more heavily harvested in this study area). Eighty-six percent of the 29 nests were in Douglas fir trees (*White 1996*).

In the California Cascade and Klamath provinces, 14 of Spotted Owl nests on private and timber company lands were external platforms; 12 were in mistletoe brooms and two were in raptor nests (*Farber and Crans 2000*). The nest tree data were combined with data from two roost trees in the following results. Mean tree diameter was 59 cm (SE = 3, range 17–34); mean tree age was 110 yr (SE = 7, range 59–184). These nest and roost trees were larger than the quadratic mean diameter of other trees (> 12 cm) in the surrounding one ha (mean = 31 cm, SE = 2).

Nest types and primary nest tree species used by Northern Spotted Owl are summarized in Table 5.3. Platform nests were more prevalent in the Eastern Cascades and California Coast Range than in other provinces, and were found in commercial forests more often than public lands of the Western Cascades, Oregon. Trees containing platform nests were generally smaller than trees containing cavity nests. Differences in nest types was not attributable solely to tree species; Douglas fir was a common nest tree species throughout the range of the Northern Spotted Owl, providing top cavities in mesic regions and mistletoe platform nests in more xeric regions.

Marshall et al. (2003) noted that approximately 90% of known Spotted Owl nests on the Applegate Ranger District of the Rogue River National Forest (Klamath province, Oregon) were in dwarf mistletoe brooms in Douglas fir trees. They compared the number of mistletoe brooms within plots surrounding 35 randomly selected nests and “nonnest” plots within 11 of the 35 nest stands. Based on a classification system that incorporated the number and type of mistletoe brooms, nest plots had more mistletoe infection and more intense infection than nonnest plots. Furthermore, 51% of Spotted Owl nests were located in mistletoe brooms that originated from the tree bole even though 8% of brooms originated from the bole. In contrast, only 20% of nests were in brooms that originated on branches even though 75% of brooms originated from branches.

6 SUMMARY

Information about Northern Spotted Owl habitat associations on private land was sparse at the time of the 1990 status review. Since then, many studies on private land have been completed and made available for public review. These studies help to broaden the scope of our knowledge throughout the subspecies' range. We also commend researchers for taking advantage of long-term Spotted Owl demographic data sets to investigate habitat associations. We encourage further exploitation of these data to measure demographic responses to habitat configuration.

Much of the information reviewed in this chapter confirmed the definition of suitable owl habitat of Thomas et al. (1990; see chapter Introduction). In the redwood zone of coastal California, Spotted Owls used younger stands for nesting than elsewhere in the range of the Northern Spotted Owl, although in the majority of young redwood stands used for nesting, residual (older) trees were present. Furthermore, as was noted in Thomas et al. (1990), structural attributes of young redwood stands are similar to attributes that accrue only in very old forests in most of the owl's range.

MCP home range estimates reported from 1990 to present were similar to those found previous to 1990. New studies (post-1990) showed that home range size was influenced by the degree of forest fragmentation and proportion of home range in mature and old forest, with increased home range size found in more fragmented landscapes and in home ranges containing a smaller proportion of mature and old forest. Primary prey species consumed by Spotted Owls was also related to home range size, with larger home ranges occurring where flying squirrels dominated the diet and smaller home ranges where woodrats dominated the diet.

In most cases, the amount of mature and old-growth forest in home ranges and core areas was greater around owl site centers than around random landscape locations, with exceptions found in the Eastern Cascades, Washington, and commercial redwood forest, California. In the Klamath province, hardwood forests were found in greater amounts at owl than random locations. When evaluated at several scales using the same data sets, differences between owl locations and random landscape locations generally diminished as distance from the owl site center (usually a roost or nest location) increased.

In the Eastern Cascades of Washington, Spotted Owls locations (200 ha) had less old-growth forest and more forest 20-64 cm dbh than random locations. Spotted owls in this study area had the lowest estimated apparent survival probability and one of the highest reproductive rates among 14 study areas throughout the range of the Northern Spotted Owl (Anthony et al. 2004; see Demography chapter, WEN study area). Further research may be warranted on whether results of fire suppression and consequent development of shade tolerant understories of pole-sized trees negatively affect spotted owl populations in this province.

Dispersing juvenile owls used mature and old-growth stands more than expected based on availability, especially during the colonization phase. Mature and old-growth stands were consistently used by territorial Spotted Owls for foraging and roosting more often than expected based on availability. At foraging and roosting sites, one or more of the following attributes tended to be greater than at random locations: canopy diversity, canopy closure, snag diameter, snag volume, dbh of large trees, amount of large woody debris.

Stand ages used for nesting by Spotted Owls varied by province and study area, with 17-100% of nests occurring in old forest among studies. At nesting sites, one or more of the following tended to be greater than at random locations: tree basal area, density of broken-top trees, number or basal area of decadent snags, volume of decadent logs.

Across provinces, the majority of Spotted Owl nests were in live trees. Cavity nests predominated in the Olympic Peninsula, Oregon Coast Range, public forest in the western Oregon Cascades. External platform nests were more prevalent in the Klamath province and commercial forests of the western Oregon Cascades and comprised the majority of nests in the eastern Cascades of Washington and both commercial and public forest in the California Coast Range. Trees containing platform nests tended to be smaller in diameter than those containing cavity nests.

Little was known about the effects of forest fragmentation on Northern Spotted Owls in 1990. Subsequent research has shown that whereas owl locations used for nesting and roosting tend to be centered in larger patches of old forest than in the available landscape, forest fragmentation is not necessarily equivalent to habitat fragmentation, at least in some portions of the Northern Spotted Owl's range (Franklin et al. 2002). Ecotones within owl home ranges may benefit Spotted Owls by providing increased prey abundance and/or availability but still need to be balanced with the presence of interior older forest (*A. Franklin, pers. comm.*).

A meta-analysis showed that owl site occupancy was positively associated with mean patch area of old forest and negatively associated with forest fragmentation, whereas studies in the redwood zone suggested diversity of cover types was higher at owl nest sites than locations not used for nesting. The degree of forest fragmentation did not appear to influence use of stands by dispersing juvenile owls.

Effects of forest fragmentation and heterogeneity on Spotted Owl survival and reproduction varied among studies. When considering both survival and reproduction, owls appeared to benefit from a mixture of mature/old forest and other cover types in the California Klamath province and from a mixture of older forests with younger forest and non-forested areas in the Oregon Coast Range. It is also noteworthy that landscape composition of stand ages was not a good predictor of reproductive output in two studies in the Oregon Cascades.

Studies on forest fragmentation and heterogeneity have provided insight into the most profound change in our understanding of habitat associations of the Northern Spotted Owl. Home ranges composed entirely of pristine old forest may not be optimal for spotted owls in the Klamath province and Oregon Coast Range, although large patches of older forest within the home range do appear to be necessary to maintain a stable population. We caution that these findings should not be extended to other areas of the subspecies' range.

7 TABLES

Table 5.1. Mean annual home range and core area sizes of Northern Spotted Owls. Data presented were estimated using 100% Minimum Convex Polygon method (MCP; all studies), and various alternate methods (some studies).

			MCP Home Range (ha)		Alternate Method					
						Home Range (ha)		Core Area (ha)		
Province and forest type	n		Mean	SE	Method	Mean	SE	Mean	SE	Source
WA Eastern Cascades	5	owls	3669	876	--	--	--	--	--	King 1993
OR Coast Range										
Mixed conifer, fragmented	5	pairs	1675	352	MMCP[a]	1154	235	--	--	Carey et al. 1992
Douglas fir	5	pairs	1569	463	MMCP[a]	1018	160	--	--	Carey et al. 1992
Douglas fir, fragmented	4	pairs	2908	595	MMCP[a]	1721	413	--	--	Carey et al. 1992
OR Coast Range										
Elliott State Forest	15	owls	1108	137	95% Fixed Kernel	842	115	87[b]	6	Glenn et al. 2004
Northern Coast Range	9	owls	2214	357	95% Fixed Kernel	1344	247	100[b]	5	Glenn et al. 2004
OR Klamath										
Mixed conifer	3	pairs	533	58	MMCP[a]	472	43	--	--	Carey et al. 1992
Mixed conifer, fragmented	6	pairs	1796	261	MMCP[a]	1208	272	--	--	Carey et al. 1992
OR Western Cascades	6	pairs	3066	1080	Adaptive Kernel	--	--	417[c]	129	*Miller et al. 1992* Irwin et al. 2000
CA Coastal redwood/Douglas fir	9	owls	786	145	95% Adaptive Kernel	685	112	98[d]	22	Pious 1995

[a] Modified Minimum Convex Polygon.
[b] Core area defined by greater than average observation location density for a given owl.
[c] Core area arbitrarily defined as 60% adaptive kernel contour.
[d] Core area arbitrarily defined as 50% adaptive kernel contour.

Table 5.2. Percentage of mature and old-growth forest (mean and SE) within circles around Northern Spotted Owl activity centers and random points or complete landscape areas.

	circle size	Owl location			Random location			Criteria for random location	Source
Province & forest type	(ha)	n	%	SE	n	%	SE		
WA Olympic Peninsula	3253	59	53	--	100	34	--	Within Olympic National Forest	Lehmkuhl and Raphael 1993
WA Cascades	314	74			1			Total 3000 km^2 study area	Hicks et al. 2003
Western Hemlock			42	11		12			
Silver Fir			44	17		20			
Interior W. Hemlock			42	14		49			
Grand fir			53	17		18			
Interior Douglas fir			44	21		18			
WA Eastern Cascades[a]	200		48			36		Within 23,832 km^2 study area	Irwin et al. in press
FMAZ 1		30	10	5	21	30	8		
FMAZ 2		56	13	4	16	22	7		
FMAZ 3		57	8	3	42	20	4		
FMAZ 4		62	6	3	18	19	5		
FMAZ 5		22	5	5	28	16	5		
OR Coast Range	200	19	36	--	19	14	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Coast Range	112	41	32	3	41	11	2	No nest found on surveyed area; at least 1260 m from nest sites	*Perkins 2000*
OR Klamath	200	21	30	--	21	6	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Klamath	118	20	45	26	20	14	20	Contained ≥ 40% forest cover	Ripple et al. 1997
OR Western Cascades	200	10	27	--	10	12	--	BLM lands surveyed for owls	Meyer et al. 1998
OR Western Cascades	260	30	78	12	30	63	20	Within Willamette National Forest	Ripple et al. 1991
OR Western Cascades	500	103	60	2	70	53	2	Centered on National Forest Land	Johnson 1992
CA Klamath	200	33	47	--	50	36	--	Within 292 km^2 area, < 1351 m elev	Hunter et al. 1995

Footnotes:

a FMAZ = Fire Management Analysis Zone.

Table 5.3. Percent of Northern Spotted Owl nest types.

			Nest type – Percent of Total				
Province	Primary nest tree species	n	Side cavity	Top Cavity	All Cavity	Platform	Source
WA Olympic Peninsula	western hemlock, Douglas fir, western red cedar	116	53	37	90	10	Forsman and Giese 1997
WA Olympic Peninsula	western hemlock, Douglas fir, western red cedar	15	67	27	93	7	Hershey et al. 1998
WA E. Cascades (north)	Douglas fir	85	11	6	17	84	Buchanan et al. 1993
WA E. Cascades (south)	Douglas fir	31	--	--	23	77	Buchanan 1996
OR Coast Range	Douglas fir	30	7	87	93	7	Hershey et al. 1998
OR Coast Range	Douglas fir	53	37	61	98	2	Thrailkill et al. 1998 [a]
OR Coast Range							
North Coast	w. hemlock, Douglas fir	12	92	8	100	0	Anthony et al. 2000
Elliott State Forest	Douglas fir, w. red cedar	22	36	9	45	55	Anthony et al. 2000
OR Klamath	Douglas fir	29	3	55	58	41	Hershey et al. 1998
OR Western Cascades	Douglas fir	27	15	78	93	7	Hershey et al. 1998
OR Western Cascades	Douglas fir	39	--	--	44	56	Irwin et al. 2000
CA Coastal	redwood, Douglas fir	97	16	14	30	65	Pious 1994
CA Coastal	redwood, Douglas fir	60	--	--	53	47	Folliard et al. 2000
CA Coastal	redwood	11	--	--	27	73	*Tanner 1999*
CA Coastal	Douglas fir, redwood, bishop pine	28	4	25	29	71	*Chow 2001*
CA Coastal	redwood, Douglas fir, bishop pine	120	--	--	12	88	Fehring et al. 2003
CA Coastal & Klamath	Douglas fir, redwood	69	20	60	80	20	LaHaye and Gutiérrez 1999
CA Klamath & Cascades	Douglas fir	29	--	--	41	59	White 1996
CA Klamath & Cascades	Douglas fir, sugar pine	14	--	--	0	100	Farber and Crans 2000

Footnotes:

a Some of the nests in this sample may have been included in Hershey et al. (1998).