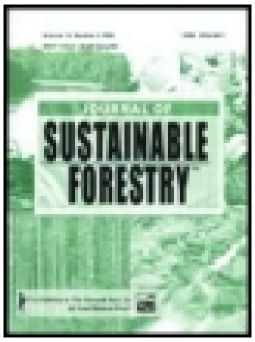

Journal of Sustainable Forestry

ISSN: 1054-9811 (Print) 1540-756X (Online) Journal homepage: https://www.tandfonline.com/loi/wjsf20

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To cite this article: Larry L. Irwin , Tracy L. Fleming & John Beebe (2004) Are Spotted Owl Populations Sustainable in Fire-Prone Forests?, Journal of Sustainable Forestry, 18:4, 1-28, DOI: 10.1300/J091v18n04_01

To link to this article: https://doi.org/10.1300/J091v18n04_01

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Are Spotted Owl Populations Sustainable in Fire-Prone Forests?

Larry L. Irwin
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ABSTRACT. We examined territory selection, occupancy and reproduction among northern spotted owls (S*trix occidentalis caurina*) relative to environmental factors influencing wildfire regimes in the eastern Cascade Mountains, Washington, USA. Territory selection was influenced positively by the amount of (a) forest with 30-70% overstory canopy cover; (b) grand fir (*Abies grandis*) and (c) riparian habitat, and negatively by (a) late-successional forest (LSF); (b) trees 13-19 cm diameter; and (c) elevation. Owl pairs in late-successional reserves (LSRs) were not more productive than those in intervening forests. Owl reproductive rates were lower in territories with more pole-sized trees and with greater annual precipitation at higher, wetter elevations and glaciated landtypes where LSF was abundant. As a result, LSF was not correlated to owl reproduction. The most productive owl pairs occurred in dry forests that were at highest risk to uncharacteristic wildfires. Short-term successional advances toward shade-tolerant, pole-sized trees may have

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Financial and logistical support was provided by the American Forest Resource Council, USDA Forest Service, and private forestry companies. The authors appreciate help from G. McCutchen, P. Murphy, S. O'Neal, C. Phillips, R. Everett, J. Lehmkuhl, W. Gaines, S. Martin, and the late T. Beebe.

Journal of Sustainable Forestry, Vol. 18(4) 2004
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Digital Object Identifier: 10.1300/J091v18n04_01

led to abandonment of 45 owl territories in mesic forests. Sustainable conservation in this area should account for physical environmental factors that influence owl population performance and reduce continuity and density of fuels. *[Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress. com> Website: <http://www.HaworthPress.com> © 2004 by The Haworth Press, Inc. All rights reserved.]*

KEYWORDS. Northern spotted owl, Cascade Mountains, wildfire regime, resource selection probability function, *Strix occidentalis caurina*, sustainable forests, late-successional forest

INTRODUCTION

Conservation reserves comprise a time-honored method of protecting natural resources (Caughley and Gunn 1996). More recently, networks of conservation reserves for protecting rare species or biological diversity generally are mapped on the basis of forest seral stage, connectivity, and area or "patch" size (Simberloff and Abele 1976). For example, Thomas et al. (1990) proposed an interconnected network of large (> 10,000 ha) habitat conservation areas for maintaining a viable, well-distributed population of northern spotted owls in the Pacific Northwest and northern California. The Forest Ecosystem Management and Assessment Team, or FEMAT (1993) expanded that conservation reserve network by mapping LSRs to account for other species associated with LSF within the geographic range of the northern spotted owl.

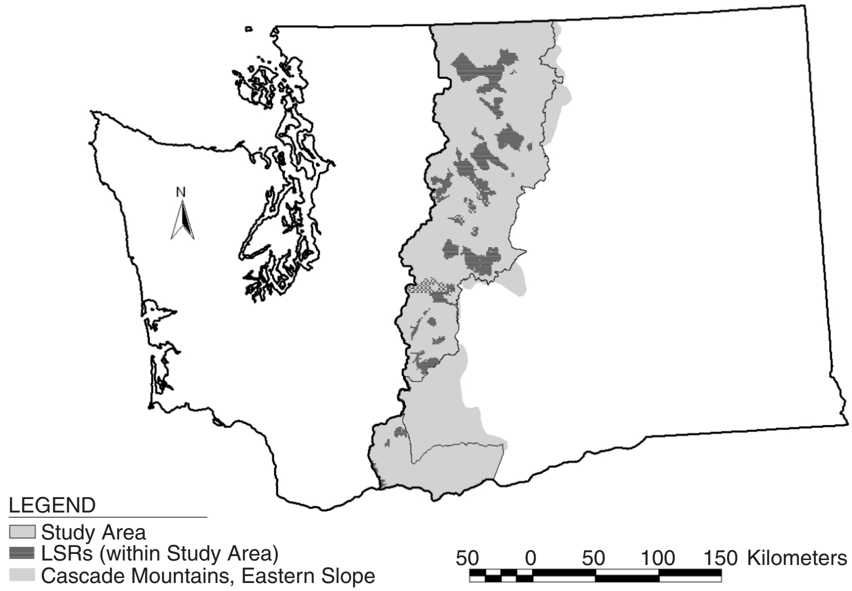
Caughley and Gunne (1996) noted that conservation reserves often have three problems: (1) they may not contain sufficient resources to support a protected species; (2) they may be host to conflicting land uses; and (3) vegetation dynamics may cause their maintenance to require manipulative management, which often generates public controversy. The FEMAT (1993) acknowledged threats to sustainability of the LSR network from large-scale wildfires and recognized the controversy associated with manipulative forest management to minimize the risks. As a result, the FEMAT (1993) recommended that silvicultural activities remain as options for manipulating forests in some LSRs. Unfortunately, little scientific information is available to guide silvicultural practices that might restore sustainability to fire-prone forests while simultaneously protecting spotted owls and supporting forest-based economies. Here, we present results from an extensive study from 1990-2000 along the eastern slope of the Cascade Mountains, Washington, where we compared spotted owl population performance in LSRs and non-reserved forests. Owl population performance was conditioned upon differences in vegetational and physical environmental conditions that influence wildfire regimes. Our goal was to support informed planning for maintaining viable spotted owl populations while restoring and sustaining healthy forests.

STUDY AREA

We chose the study area in part because forests on the eastern slope of the Cascade Mountains differ substantially from those in western Oregon and Washington. East-slope forests developed in response to greater variability in climate, topography and soils, as well as more extensive history of montane glaciation than westside forests (Del Moral 1972, Lillybridge et al. 1995). Following European settlement, numerous multiple-aged, mixed-composition forests resulted from overstory removals or selective timber harvests (Richards 1989, Camp et al. 1997). Such vegetative and geophysical diversity may have influenced the relatively high diversity of prey exploited by spotted owls in this area (Richards 1989). Moreover, nearly all eastside forests were influenced historically by wildfires (Agee 1994, Camp et al. 1997, Everett et al. 2000). Since 1910 many eastside forest stands became increasingly comprised of dense, shade-tolerant tree understories as a result of fire suppression (Lehmkuhl et al. 1995, Everett et al. 2000). Such variable conditions provided the setting for a natural experiment to examine the influences of the physical environment, vegetation conditions and altered fire regimes on spotted owl population performance.

The study area spanned 23,832 km^2 from near the Canadian border south to the Oregon border (Figure 1). The study area included 4 owl territories in North Cascades National Park, 221 on the Wenatchee and Okanogan National Forest and associated state and private timberlands, and 29 on the Gifford Pinchot National Forest and associated state and private timberlands. It encompassed several forest zones: Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), Grand fir, Western hemlock (*Tsuga heterophylla*), and Subalpine fir (*Abies lasiocarpa*). These zones supported vegetation associations (Franklin and Dyrness 1973, Williams and Smith 1990) that were frequently interspersed as a result of varying topography, geological structure, precipitation and soils. Also, current forests exhibit effects of widespread fire-control and previous timber harvest practices. These effects include epidemic levels of forest pathogens, insects and diseases, and dense

FIGURE 1. Map of Washington State, including the study area and forest-covered lands east of the crest of the Cascade Mountains from near the Canada border in the north to the border of the state of Oregon. Study locations did not include timberlands of the Yakama Indian Nation, which lies in the south-central part of the study area. Also shown are the late-successional reserves (LSRs) that occur within the study area.



understories of grand fir or Douglas-fir (Everett et al. 1994, Everett et al. 1996, Camp et al. 1997, Méndez-Trenneman 2001).

OBJECTIVES

We developed four objectives:

1. Construct a process-based resource selection probability function (RSPF) model that could be used to predict carrying capacity for spotted owls across the forested landscape (Boyce et al. 1994, Boyce and McDonald 1999) based upon factors influencing selection of territories (i.e., areas owls defend against intrusions by conspecifics).
2. Determine biotic and abiotic factors that influence the frequency with which territories are occupied by pairs of owls (i.e., occupancy).

3. Identify forest structural conditions and physical environmental factors that influence longterm reproductive performance within territories.
4. Assess sustainability by relating findings to the LSR strategy and fire regimes.

METHODS

Resource Selection Probability Function

A resource selection function (RSF) is defined as any mathematical function that is proportional to the probability of use by an organism (Manly et al. 2002). The units being selected are compared either to unused areas or to availability across the landscape using a binomial generalized linear model. We compared conditions at 189 owl territories with conditions at randomly available landscape locations (n = 125) because we could not be certain that random landscape locations did not contain owl territories (Manly et al. 2002). A RSF can be converted to a RSPF by accounting for sampling fractions of used and available resource units (Manly et al. 2002:100). When linked to a geographical information system (GIS) and forest growth models, RSPFs can be used to estimate current and future carrying capacity and thereby provide powerful tools for land-management planning (Boyce and Waller 2000, Boyce et al. 2003).

We reviewed ecological literature to identify biotic factors that should be included in RSF models. For example, forest stands that are relatively near streams (i.e., riparian zones) should contain a greater abundance of prey via a greater expression of understory vegetation (Carey et al. 1992, Peffer 2001), and thereby, influence territory selection (Irwin 1994, Irwin 1998, Hicks et al. in press). We included forest structure (represented by dbh classes) because it has long been assumed to be a major determinant of distribution and habitat selection by forest bird populations (MacArthur 1958, Thomas 1979). This assumption was considered particularly applicable to northern spotted owls (Thomas et al. 1990) because of strong associations among owls, their prey and such forest structures as large trees (Forsman et al. 1984) and snags, downed woody debris and understory vegetation (Carey et al. 1992, Irwin et al. 2000).

Abiotic, or physical environmental factors also have been shown to influence wildlife distributions and abundances (Irwin 1998, Pearce et al. 2001) including territory selection by spotted owls (Haufler and Irwin 1993, Irwin 1994, Meyer et al. 1998). For example, precipitation or soil fertility could determine abundance or availability of the owl's mammalian prey base, and thereby constrain owl population performance (Newton 1979:290, Franklin et al. 2000). Recent authors (Amundsen and Jenny 1997, Hansen and Rotella 1999, Huston 1999) recognized that topography, soils, weather and disturbance regimes determine net primary productivity and biological diversity. Hicks et al. (in press) found that site index, an indicator of productivity, influenced territory selection by spotted owls in a portion of our study area. We presumed that elevation would also be a factor due to a shift from mixed forests of ponderosa pine and Douglas-fir at low elevations to more true fir, which has less prey biomass in similar vegetation types in southwestern Oregon (Carey et al. 1992).

We accounted for the influences of the physical environment by including elevation, standard deviation of elevation, average annual precipitation, the amount of a spotted owl territory contained in riparian zones (defined as habitats within 100 m of streams), and landtype association. Landtype association is a fundamental unit of land classification that incorporates the expression of dominant soil-forming processes (e.g., glaciation, mass wasting, fluvial deposition, etc.) and soil parent materials (Wendt et al. 1965, Wertz and Arnold 1972, Zonneveld 1989). We accounted for interactions among biotic and abiotic factors using the fire management analysis zone, or FMAZ concept (USDA Forest Service 1982). FMAZ is a composite, cartographic descriptor based on standardized criteria for estimated historic frequency of fire ignitions and fire-return intervals, along with broad estimates of fuel loading and associated factors that influence the rate of fire spread and probability of crown fires. The study area contained five FMAZs, which varied with fire regime, topography, elevation, vegetation zone and average annual precipitation (Table 1).

The size of territories defended by spotted owl is unknown. We used circular 200-ha sampling units centered on nest sites of owl pairs as a conservative unit to approximate territories because such sampling units provide strong statistical discrimination between used and available areas (Hunter et al. 1995, Ripple et al. 1997, Bingham and Noon 1997, Meyer et al. 1998). The average distance between spotted owl nest sites in our study region is less than 2400 m, suggesting territories are probably not larger than 450 ha. Meyer et al. (1998) suggested that characteristics of an inner core or 200 ha may influence selection of territories by spotted owls.

TABLE 1. Major fire management analysis zones (FMAZ) for the Wenatchee National Forest, Washington.[a]

FMAZ	Ignitions/ 400 ha/yr	Precip. cm/yr	Topography	Dominant Vegetation Types
1	0.102	40-90	foothills	pine/fir transition
2	0.074	40-90	foothills	pine/fir transition
3	0.044	100-180	montane, 41-55% slopes	mixed conifer
4	0.046	100-180	montane, 26-40% slopes	mixed conifer
5	0.030	> 180	subalpine, 41-55% slopes	western hemlock, subalpine, alpine

[a] Based on information on file at Wenatchee National Forest, Washington, and B. Keleman (pers. comm., Wenatchee National Forest).

Using several sources, we obtained GIS data layers on forest vegetation for a majority of the study area and acquired information on physical environmental variables throughout the study area. We mapped the study area using GIS-based information generated by the Columbia Basin ecosystem assessment (Quigley et al.1996, USDA Forest Service 1996), which we ground-truthed using forest inventory information *obtained* from private timber companies. The more detailed GIS maps of tree dbh classes and physical environmental factors were based upon pooled geographic data derived primarily from processed Landsat satellite images (using supervised classifications and 4-ha minimum mapping units), and interpreted aerial photos (typically 1:15,840 scale). We used ground-truthed forest inventory information to supplement and verify the image processing, as well as predictive mapping that was based upon terrain, climate and elevation. We mapped FMAZs with assistance from Wenatchee/Okanogan and Gifford Pinchot National Forest fire and wildlife staff officers as well as GIS personnel from private companies. Because of minor changes in forests caused by timber harvesting or forest growth during the study, we used estimates of vegetation conditions available during the mid-point of the study (1994-95). Six spotted owl territories were modified by > 15% via logging during the study; these and 12 territories that were burned intensively in 1994 were not used for analyses.

Following Manly et al. (2002), we used logistic regression to develop coefficients for the several independent vegetative and abiotic variables shown in Table 2, similar to Meyer et al. (1998) and Niemuth (2003).

Here the regression estimates the RSF, which is the relative probability that a landscape location contains an owl territory:

$$\hat{G} = \exp(z)/\{1 + \exp(z)\},$$
where z is the familiar linear equation (1)

$$z = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i. \quad (2)$$

We included unimodal (quadratic term) and quasi-threshold ($\log_e$) transforms for tree-dbh classes to account for potential non-linear relationships (Franklin et al. 2000). Given the transforms and a large number of abiotic and biotic factors, literally hundreds of models could be developed and tested against data, some of which could be spurious. We guarded against such data dredging by reducing the number of influential variables via literature reviews, ANOVAs, and using an information theoretic analytical process (Burnham and Anderson 2002). We exam-

TABLE 2. Variables used in the RSF analyses.

Variables	Group acronym (unit)	Description
		Vegetation Structure or Composition
1-5	DBH (cm)	Hectares not-forested or conifers < 13, 13-19, 20-64, or > 64 cm dbh
6-10	CC class (%)	Hectares < 10, 10-29, 30-49, 50-70, or > 70% canopy closure
11-15	COMP (ha)	Ponderosa pine ($_{PINE}$), Douglas-fir ($_{DFIR}$), Grand fir ($_{GFIR}$), Subalpine fir ($_{SAF}$), Mountain hemlock ($_{MHEM}$), other
		Physical Environmental Factors
16-21	PCP (cm)	Precipitation zone < 10, 10-16, 17-23, 24-31, 32-38, > 38 cm
22-26	ELEV (m)	Elevation class < 600(1), 601-900(2), 901-1200(3), 1201-1500(4), > 1500 m (5)
27	SDELEV	Standard deviation of elevation
28-32	LTA	Landtype association–presence-absence of glacial cirque (LTA_1), glacial trough (LTA_2), glaciated montane slope (LTA_3), montane slope (LTA_4), structurally controlled mountain slope and all other landforms, including stream bottom, plateau, lakes, low relief glaciated lands (LTA_5)
		Composite Factors
33-37	FMAZ	Fire management analysis zone (classes 1-5)
38	RIP	Riparian or streamside zones (ha)

ined influences of vegetative factors first, and subsequently added physical environmental covariates. The analytical process involved identifying the most plausible *a priori* combinations and applying change–in Akaike's information criterion (Akaike 1973), corrected for small samples (Burnham and Anderson 2002:66), or ΔAICc to identify the most parsimonious model(s).

We estimated the RSPF from the ΔAICc best RSF by (1) estimating the sampling fractions, P_a and P_u, where P_a is the proportion of available 200-ha units sampled and P_u is the proportion of used 200-ha units, that is, fraction of total owl territories; and then (2) subtracting the quantity, $\log_e[(1 - P_a)P_{u/}P_a]$, from the constant, β_o, in the RSF, following Manly et al. (2002:100). We estimated that 11,916 200-ha units could fit into the 23,832 km^2 study area, so P_a is 0.010 (i.e., 125/11916). If we assume the total number of owl territories (350) identified by various researchers and biologists working in the eastern Washington Cascades is correct, then P_u is 0.54 (189/350). Thus, the RSPF is estimated by subtracting -4.02 from the constant term in the best RSF {i.e., $\log_e[(1.0 - 0.01)/0.54/0.01] = -4.02$}.

Occupancy Rate

We monitored spotted owls at their territories following procedures established by Forsman (1983) and Franklin et al. (1996). We visited owl territories and nest locations a minimum of 6 times per year until field objectives were met. Occasionally, we made additional visits to verify occupancy by pairs, reproductive status or the number of young.

Franklin et al. (2000) demonstrated that seasonal precipitation and forest conditions influenced spotted owl population performance. Therefore, we wanted to determine if tree dbh classes, physical environmental factors and land-use status influenced the number of years that territories were occupied by spotted owl pairs. Land survey information defined by the U.S. Forest Service Regional Ecosystem Office in implementing FEMAT (1993) was used to identify percentages of land-use designations for each owl territory. We labeled an owl territory to be in a LSR if the majority of an analytical unit was designated as a late-successional reserve. Similarly, we labeled an owl territory to be in the forest matrix if ≥ 50% of the 200-ha sampling circle was outside a LSR.

We used one-way ANOVA to evaluate factors that influenced the number of years that territories were occupied by spotted owl pairs. Spotted owl territories were assigned to occupancy groups as follows:

infrequently occupied, including those territories that were occupied by an owl pair < 2 of the 11 years; intermittently occupied, for territories occupied by owl pairs 2-5 years; and consistently occupied, for territories that were occupied by a pair of owls for > 5 years and vacant ≤ 2 years.

Forty-five territories monitored since 1990 were abandoned by spotted owls the last 3 years of our study, although none of the territories had been logged or burned. We used t-tests to compare vegetation and environmental conditions at abandoned territories with conditions at territories where we found at least 1 owl at the end of the study period.

Reproduction

Because FEMAT (1993) designed the LSR network to contain abundant and less fragmented LSF (i.e., presumed high quality habitat for northern spotted owls), we predicted that owl reproductive performance in LSRs would be greater than that of owls living in non-reserved forests, or "matrix," between LSRs. To test that prediction, we compared average reproductive rates of spotted owl pairs (a) living in LSRs with reproductive rates of pairs that occupied matrix forests and (b) among forests with different inherent fire regimes, as represented by the 5 FMAZs. We developed multiple regressions to identify forest structural classes and abiotic environmental factors that were correlated with the average number of owlets produced at territories over the 11 years. Factors included those described above for occupancy by pairs. We used ANOVA to compare reproductive success of owls in LSRs with those in matrix forests and to compare reproductive rates among owls in different FMAZs, following Ramsay and Schafer (1997).

RESULTS

Resource Selection

The majority (>50%) of the forested landscape sampled at random in our study area occurred in steep, highly-dissected topography or high elevations in FMAZs 3 and 5, whereas a majority of spotted owl territories occurred in more rolling, foothills topography in FMAZs 2 and 4 (Table 3), where fire frequencies were relatively high. We found significant variability in distributions of tree dbh classes among the 5 FMAZs at random landscape locations, whereas such structural conditions at

TABLE 3. Average percentages of tree-diameter classes (sd) within 200-ha sample units centered on spotted owl nesting sites and random landscape locations in fire management analysis zones of the eastern Washington Cascades.

Dbh Class	Fire Management Analysis Zone					
(cm)	1	2	3	4	5	P-value[a]
			Spotted owl territory locations			
> 64	10.0 (5)	13.2 (4)	7.8 (3)	5.5 (3)	5.4 (5)	0.443
20-64	48.4 (6)	54.5 (5)	61.0 (5)	63.3 (4)	55.6 (8)	0.328
13-19	19.1 (5)	12.5 (3)	10.2 (3)	12.7 (3)	21.6 (7)	0.605
< 13	22.4 (6)	19.7 (4)	20.9 (4)	18.5 (4)	17.3 (6)	0.976
Number	30	56	57	62	22	227
Percent	13.2	24.7	25.1	27.3	9.7	
			Random landscape locations			
> 64	30.0 (8)	22.4 (7)	20.1 (4)	19.1 (5)	16.2 (5)	0.807
20-64	28.1 (5)[b]	35.1 (9)	35.6 (6)	33.5 (8)	35.6 (7)	0.044
13-19	10.3 (6)	9.9 (5)	19.6 (4)	16.9 (6)	22.5 (6)	0.803
< 13	32.0 (7)	32.6 (7)	24.6(5)[b]	30.5 (7)	25.7 (6)[b]	0.037
Number	21	16	42	18	28	125
Percent	16.8	12.8	33.6	14.4	22.4	

[a]Based on one-way ANOVA comparing among FMAZ in each dbh class.
[b]Significantly different ($P < 0.10$) from other column values within corresponding dbh class.

owl territories were more consistent among FMAZs. Across the study area at random, the greatest amounts of LSF, or those trees > 64 cm dbh, occurred in FMAZs 1 and 2. Despite that, average 200-ha owl territories contained less forest dominated by trees > 64 cm dbh than random landscape locations, especially in the wetter, higher-elevation zones in FMAZs 3-5 (Table 3). In general, $\geq$ 48% of the owl territory circles were dominated by trees 20-64 cm dbh, while $\leq$ 36% of random analysis circles fell in that category.

Logistic regression analyses confirmed that forest vegetation conditions, namely composition, dbh class, overstory canopy cover class and physical environmental features discriminated spotted owl territories from random landscape locations (Table 4). We found little support for RSF models containing unimodal or pseudo-threshold relationships

TABLE 4. Best resource selection functions fitted by logistic regression to discriminate between spotted owl territories and random landscape locations, using 200-ha circular sampling units.

Model	Variables included in equation	ΔAICc
1) Model 3 − LTA_2 − $COMP_{MHEM}$		0.00
2) Model 3 − LTA_2		0.65
3) −LTA_3 + $ELEV_{2,3,4}$ − $DBH_{13\text{-}19,\,>64}$ − $CAN_{10,30,70}$ + $COMP_{GFIR}$ + RIP		1.92
4) Model 3 − $DBH_{20\text{-}64}$		3.10
5) Model 3 − LTA_2 + $FMAZ_2$ without $COMP_{GFIR}$		3.84
6) Model 3 − LTA_2 without $COMPG_{FIR}$		4.59
7) Model 3 − LTA_2 + $FMAZ_2$ + $FMAZ_3$ − $DBH_{20\text{-}64}$ − $COMP_{MHEM}$ − $COMP_{SAF}$		5.39
8) Model 3 − LTA_2 − $COMP_{MHEM}$ without $ELEV_{2,4}$		6.31
9) −LTA_3 + $ELEV_{2,3,4}$ − $DBH_{13\text{-}19}$ − $CAN_{10\ \&\ 30}$ + $COMP_{GFIR}$ + RIP		7.29
10) Model 9 without LTA_2		7.46
11) $FMAZ_2$ − $LTA_{2,3}$ + $ELEV_{2,3,4}$ − $DBH_{13\text{-}19}$ − $CAN_{10,20,30}$ + RIP		8.69
12) Model 11 + $SLOPE_{40}$		9.74
13) Model 11 + $FMAZ_1$ + $(DBH_{13\text{-}19})^2$ + $(DBH_{>64})^2$ + $COMP_{GFIR}$		9.98
14) Model 11 + NONFOR		10.83
15) Model 11 without CAN_{70}		11.92
16) Model 11 − $DBH_{>64}$ and without $DBH_{13\text{-}19}$ and CAN_{70}		12.07
17) Model 11 − $LN(DBH_{>64})$ and without $DBH_{13\text{-}19}$		13.65
18) Model 11 + $(DBH_{13\text{-}19})^2$		13.78
19) Model 11 + $LN(DBH_{20\text{-}64})$ and without $DBH_{13\text{-}19}$		14.50
20) Full model		56.38

(e.g., Models 13, 17,18, and 19 in Table 4). Compared to available conditions, owl territories were more likely to occur in areas with greater amounts of riparian zones at elevations from 600-1,500 m, moderately dense grand fir forests (30-70% canopy cover) and with smaller amounts of areas comprised of trees 13-19 cm dbh. Random landscape locations in glacially-scoured landtypes (LTAs 2 and 3) were less likely to contain owl territories than locations on montane slopes that presumably contained deeper, more productive soils. In practice, models within 2

AIC units of the top model should be considered plausible models to account for variation in data. The top 3 models each contained variables for landtype association and predominant tree species, so we chose the model with lowest AICc as "best" model. The best model is shown in Table 4 as RSF model (1), which correctly classified 82% of the random and owl sites overall. After adjusting for sampling fractions, the estimated RSPF becomes

$$\hat{S} = \exp(z^*)/\{1 + \exp(z^*)\}, \text{ where}$$

$$z^* = 4.99 - 1.02(LTA_2) - 0.92(LTA_3) + 2.73(ELEV_2) + 2.18(ELEV_3) + 2.14(ELEV_4) - 0.007(DBH_{13\text{-}19}) - 0.009(DBH_{>64}) - 5.86(CC_{<10}) - 7.82(CC_{10\text{-}29}) - 8.0(CC_{>70}) + 1.08(COMP_{GFIR}) - 7.91(COMP_{MHEM}) + 4.15(RIP). \quad (3)$$

Factors Influencing Occupancy

After the initial year (1990), when we surveyed 119 owl territories, we monitored an average of 180 spotted owl territories per year. We obtained vegetation structure and environmental information for 168 of those territories. We were unable to detect any significant differences among the 3 occupancy-rate types (infrequently-, intermittently-, or consistently occupied by owl pairs) relative to tree dbh classes. However, the frequency of occupancy by owl pairs was associated with abiotic factors and varied among the FMAZs. The frequency of occupancy decreased steadily with increasing elevation and with increasing precipitation, was highest in FMAZs 1, 2, and 4 and was lowest in FMAZs 3 and 5.

For 45 owl territories that were vacant the last 3 years of the study we found lower amounts of forest in the seedling and sapling stages (< 13 cm dbh) than at territories that contained 1 or more owls (8.5% vs. 19.1%, P = 0.047). We also found, perhaps correspondingly, greater amounts of forest dominated by pole-sized trees (13-19 cm dbh) at abandoned territories (21.7% vs. 11.9%, P = 0.049). We found no differences in amounts of other diameter classes or canopy cover classes between vacant and occupied territories.

Factors Influencing Reproductive Success

Owl reproductive success was strongly associated with abiotic environmental conditions. Average reproductive rate declined with increasing annual precipitation and with increasing elevation (Table 5). Reproductive success also differed significantly ($P < 0.01$) among owl territories in the various landtypes: those in glacially scoured landforms ($N = 63$) averaged 0.38 ± 0.07 (se) fledglings per year, whereas those in non-glaciated montane slopes ($N = 65$) averaged 0.57 ± 0.06 (se) fledglings per year. Multiple regression analyses confirmed that tree dbh classes also influenced reproductive success, but the regressions accounted < 15% of the variation in reproductive output (Table 6). In regressions that included tree-diameter distributions only, reproductive success increased with increasing area of trees that were 20-64 cm dbh and > 64 cm dbh (Model I in Table 6). Although highly statistically significant, that model accounted for only 12% of the variation in reproductive success. When we broadened the analyses by adding precipitation zone, the 20-64 cm diameter class became non-significant. A reduced-parameter model (Model III in Table 6) with precipitation zone and large trees accounted for 12% of the variation in reproductive success.

We obtained information that allowed comparisons of reproductive output among owls at 108 territories relative to land-use status. Reproductive success among owls at 81 territories in LSRs (0.60 ± 0.04

TABLE 5. Spotted owl reproductive rate relative to precipitation and elevation zones, eastern Washington Cascades, 1990-2000.

	No. territories in sample	Average young/year (se)
Precipitation zone (cm/yr)		
< 51	4	0.96 (.15)
51-75	52	0.55 (.06)
76-125	48	0.57 (.05)
126-200	26	0.40 (.09)
201-300	8	0.26 (.14)
> 300	7	0.10 (.15)
Elevation zone (m)		
600-914	7	0.88 (.15)
915-1219	40	0.54 (.06)
1220-1524	73	0.50 (.05)
1525-1829	37	0.39 (.07)
> 1829	1	0.00 (.00)

TABLE 6. Regressions of factors influencing average spotted owl reproductive success on the eastern slope of the Washington Cascades, based on conditions in 200-ha circles.

Variable	Regression coefficient	t-value	Probability
	Model I. Vegetative factors: Diameter classes		
Intercept	0.156	1.56	0.121
< 13 cm dbh (%)	0.134	0.76	0.448
20-64 cm dbh (%)	0.432	3.81	0.000
> 64 cm dbh (%)	0.469	2.75	0.007
R-squared: 0.116			
	Model II. Reduced Diameter-class model		
Intercept	0.208	2.82	0.005
20-64 cm (%)	0.385	4.05	0.000
> 64 cm (%)	0.424	4.05	0.000
R-squared: 0.112			
	Model III. Mixed model: Structure plus precipitation zone		
Intercept	0.816	7.15	0.000
> 64 cm (%)	0.505	1.78	0.078
Precipitation zone	−0.112	3.19	0.002
R-squared: 0.113			

young/yr) was not greater ($P = 0.245$) than reproductive performance of owls at 27 non-reserved locations in the federal matrix and private timberlands (0.72 ± 0.06 young/yr). To ensure that survey effort or occupancy status did not bias that comparison, we restricted the analysis to sites that had been surveyed > 7 years and had owl pairs > 3 of those years. Owl pairs at 59 such consistently-occupied territories in LSRs did not produce more young per year, on average, than owl pairs in 25 matrix locations that also were consistently occupied by owl pairs (0.67 ± 0.05 vs. 0.75 ± 0.06, $P = 0.439$).

Spotted owl reproductive rates varied among the FMAZs. Owl pairs living in drier, ponderosa pine/Douglas-fir forests in FMAZs 1 and 2 at the foot of the Cascade Mountains and those in relatively gentle topography in grand fir mixed coniferous forests in FMAZ 4 exhibited the highest rates of reproduction. Those pairs in deeply incised, glaciated landforms in grand fir forests in (FMAZ 3) demonstrated intermediate levels; and those in moist western hemlock and subalpine forests (FMAZ 5) showed lowest levels (Table 7).

The changes in weights of the vegetation variables when precipitation was added in Table 6 suggested that interactions existed between vegetation conditions and precipitation and elevation, or both. To account for such potential interactions, we restricted multiple regression models to FMAZs 1 and 2 combined, and FMAZs 3 and 4. Doing so allowed comparisons among owl territories located within similar elevations, vegetation types and precipitation zones. Sample sizes for owl territories in FMAZ 5 were too small for similar analyses. For owl pairs in 42 territories in FMAZs 1 and 2, reproductive rates were not associated with tree dbh classes (Table 8). For 77 owl territories in FMAZs 3 and 4, average reproductive success increased with increasing proportions of trees > 64 cm dbh, but this class accounted for only 12% of the variation in reproductive success.

DISCUSSION

Habitat selection generally is believed to be influenced by multiple and interacting abiotic and biotic factors (Partridge 1978). Indeed, we found that forest vegetation conditions interacted with physical environmental factors to influence territory selection by spotted owls. Compared to conditions available at random, spotted owl territories contained moderately dense forest canopies (30-70% overstory cover) at low-to intermediate elevations and successionally intermediate forests dominated by trees 20-64 cm dbh. These results generally conform to previous reports (e.g., Forsman et al. 1984, Thomas et al. 1990, Haufler and

TABLE 7. Reproductive success among spotted owls in Fire Management Analysis Zones (FMAZ), eastern Washington Cascades, 1990-2000 ([a] statistically different at $P < 0.05$).

FMAZ	Dom. vegetation	No. of owl sites	Average young/Year (se)
1	P. pine/Douglas-fir	26	0.634 (0.076)
2	Douglas-fir/P. pine	22	0.621 (0.082)
3	Grand fir (incised)	19	0.363 (0.089)[a]
4	Grand fir zone (rolling)	62	0.542 (0.049)
5	W. hemlock/subalpine	15	0.139 (0.100)[a]

TABLE 8. Correlations of habitat structural factors (area within 200-ha circle) with average spotted owl reproductive success, constrained to sites in FMAZs 1 and 2 combined and also in FMAZs 3 and 4 combined.

Variable	Regression coefficient	T-value	Probability level	Regression
	FMAZ 1 and FMAZ 2 Sites (N = 42, R-squared = 0.12)			
Intercept	−0.606	2.270	0.029	0.179
13-19 cm trees	−0.009	1.238	0.223	
20-64 cm trees	0.005	0.192	0.849	
> 64 cm trees	−0.007	1.032	0.308	
	FMAZ 3 and FMAZ 4 Sites (N = 77, R-squared = 0.12)			
Intercept	−0.062	0.192	0.848	0.024
13-19 cm trees	0.002	0.880	0.382	
20-64 cm trees	0.656	1.846	0.069	
> 64 cm trees	0.004	2.216	0.030	

Irwin 1993, Meyer et al. 1998), although extensive areas with large-diameter trees did not appear as important at the landscape level in our study. Yet, large trees are important in nest site selection at the within-stand level in our study area (Buchanan et al. 1995) and in reproductive success in some of the FMAZs (3 and 4).

In concert with GIS and forest-growth models, the RSPF can be used as a decision-support tool to evaluate alternative forest management strategies (Boyce et al. 1994, Boyce and McDonald 1999) by predicting carrying capacity for spotted owls across the existing forested landscape. This can be accomplished by averaging probabilities for 200-ha units in a moving-window procedure in GIS (Hicks et al. in press). Future carrying capacity can be estimated by modifying the GIS landscape according to a forest management prescription and an appropriate forest-growth model, and then subsequently re-applying the RSPF. Probability values for each 200-ha sampling unit also can be modified to express reproductive potential for population viability assessments (Boyce et al. 1994).

Our data suggest that large-scale attributes of the physical environment constrained smaller-scale relationships between owl population performance and vegetation structural conditions. Important physical factors influencing rates of occupancy and reproductive success included annual precipitation, elevation, glacially-scoured landtypes and

FMAZ, the latter a composite that included forest zone. Owl pairs living in LSRs did not show greater reproductive output than owls in matrix forests, despite the fact that LSF was more extensive in LSRs. In FMAZ 4 spotted owl pairs with territories that contained more forests with large trees (probably Douglas-fir) exhibited greater reproductive output, whereas trees 13-20 cm dbh (probably shade-tolerant grand fir) may have exerted a negative influence on long-term occupancy. On the other hand, relatively small and intermediate trees (<13 cm dbh and 20-64 cm dbh), likely Douglas-firs, were correlated positively with owl reproductive performance in FMAZs 1 and 2. In those 2 zones, large trees were primarily ponderosa pines.

The constraining effects of abiotic environmental factors, correlations with FMAZs and our observations that small-diameter trees exerted contrasting effects in different forest types (i.e., changes in tree composition) indicate that a modified view is warranted for assessing habitat quality for northern spotted owls. Assessments of spotted owl habitat quality based on remotely-sensed LSF or forest age classes are inadequate because forest vegetation cannot accurately represent the multivariate nature of interactions between spotted owl populations, vegetation structure and the physical environment (Irwin 1994). For example, we observed a weak statistical relationship between spotted owl reproductive performance and amounts of LSF, as did others (Bart and Forsman 1992, Lehmkuhl and Raphael 1993, Raphael et al. 1996, Meyer et al. 1998). LSF was correlated with productivity of spotted owls only in FMAZ 3 and 4, yet that correlation accounted for less than 15% of the variation in reproductive success.

We suggest that habitat *quality* for northern spotted owls involves physical environmental influences and unmapped vegetative structural conditions and vegetation composition, which are not incorporated when broadly mapping LSF via satellite images or aerial photos. The forests where owls exhibited the highest reproductive success included Douglas-fir/ponderosa pine and mixed grand fir/Douglas-fir stands that were primarily in Oliver and Larson's (1990) stem-exclusion and stand re-initiation phases of succession (Buchanan 1991). More than half of the owl nests in this area occur in forest stands less than 130 years of age (Buchanan et al. 1995). Forests with lowest occupancy and reproduction rates by owl pairs included highly dissected topography and glaciated landtypes in FMAZ 3 and in mesic true fir and subalpine fir associations in volcanically-derived landtypes in FMAZ 5.

Strong differences in owl reproductive success among the FMAZs suggest that the FMAZs integrate abiotic environmental factors that directly or indirectly influence spotted owls. These factors probably express themselves through constraints on prey abundance and/or availability or by influencing energy balances of owls. Franklin et al. (2000) and Weathers et al. (2001) concluded that LSF provides favorable microclimates and thereby helps owls to maintain energy balance by minimizing the effects of inclement weather in summer or winter. For example, FMAZ 5 includes owl territories nearest the Cascades crest, where the forests receive relatively high amounts of annual precipitation. There, owl reproduction is low, although the old-growth trees there may confer survival value to adult owls. Excessive precipitation has been shown to decrease reproductive success among spotted owls (Franklin et al. 2000), and deep, lingering snow blankets in FMAZs 5 and FMAZ 3 may protect all but arboreal prey animals well into the nesting season. In those areas, it seems possible that adult females enter the nesting season in comparatively poor condition during years with high winter precipitation. In some years, nesting may be precluded or terminated by late spring rain-or snowstorms that disrupt energy balances. Elevation, by itself, appears less of a factor: some owl territories in FMAZs 2 and 4, where reproductive success was high, actually were higher in elevation than owl territories in FMAZs 3 and 5.

Implications for Conservation and Sustainable Forest Ecosystems

Setting aside conservation reserves to protect rare species only works if the reserves meet the needs of the species of interest and will be sustainable over the long term (Caughley and Gunne 1996). In the eastern Cascades, important questions linger regarding the longterm sustainability of the LSR network (Everett et al. 2000) because altered fire/insect/disease disturbance regimes have changed tree, stand and landscape characteristics (Covington et al. 1994, Everett et al. 1994). Pre-settlement fires there consistently could be characterized as ground fires, and there is little evidence for landscape-level catastrophic fires (Everett et al. 2000). Several large, intensive wildfires burned >56,500 ha in 1994 (Everett et al. 1995, Everett et al. 2000), destroying at least 12 spotted owl territories and moderately affecting many others (Gaines et al. 1997, Bevis et al. 1997). Some LSRs contain forests where spotted owl productivity is low, and other LSRs where owls are most productive exhibit the greatest risk to catastrophic wildfire. As a result, much of the LSR network and the owl subpopulations intended for protection are not sustainable over the long term. Therefore, forest and wildlife managers on the eastern slope of the Washington Cascades are challenged with the paradox of restoring altered forest ecosystems while meeting conflicting land use objectives for various resources, including both spotted owl recovery and timber production.

To illustrate the extent of the quandary, Irwin and Thomas (2002) overlaid maps of wildfire condition ratings (Schmidt et al. 2002) with spotted owl locations in our study area. Wildfire condition classes involve the relative departure from historic ranges of variation in wildfire disturbance regimes. Forests that deviate substantially from historical ranges of variation, such as by missing more than 2 fire cycles, are most at risk to uncharacteristic or catastrophic wildfire. Irwin and Thomas (2002) found that 44% of the spotted owl territories occurred in forests where fire regimes have been significantly altered (fire condition class 3). Similarly, over half of the forested area contained in LSRs appears at risk, with 31% occurring in condition class 3 and 23% in forests in condition class 2 with moderately altered regimes. The most serious situation occurs in FMAZs 1 and 2, where 89 of 93 owl-territory locations were classified as being in forests with moderate or significantly altered fire regimes.

Insect epidemics contribute to the wildfire risk: a Western spruce budworm (*Choristoneura occidentalis*) epidemic has occurred on large portions of the study area since at least 1994, and continues to spread. The spruce budworm defoliates large and small-diameter trees, particularly grand fir. The resulting mortality contributes to ground fuels and standing dead thickets that serve as ladder fuels that could conduct ground fires into forest crowns (Méndez-Trenneman 2001). The defoliation and tree mortality may also directly reduce habitat quality for spotted owls.

Our study is the first to acquire evidence that relatively short-term forest successional changes, namely increases in amounts of small-diameter trees, may lead to owl population changes via abandonment of territories and reduced reproductive success. There is a widespread successional trend from stand dominance by seral Douglas-fir trees toward climax, shade-tolerant grand fir trees (Mèndez-Trenneman 2001). In addition, northern spotted owl populations can change solely due to climatic influences (Franklin et al. 2000), although competition from barred owls (*Strix varia*) in mesic forests (Herter and Hicks 2000) and defoliation by the Western spruce budworm may have contributed to the changes.

Understory shrubs important to small mammals are crowded out by dense small-diameter trees during the "ecological crunch" phase of forest growth (Carey and Curtis 1996). Understory shrubs are crowded out within a few decades after regeneration in similar grand fir forests in northern Idaho (Irwin and Peek 1979). Also, insect-and-disease weakened Douglas-firs are slowly being replaced by grand fir, which is not as valuable to spotted owls for nesting (Buchanan 1991, Buchanan et al. 1993). A custodial conservation strategy for northern spotted owls that promotes contiguous areas of dense, multi-layered forests (i.e., LSRs) cannot be viewed as sustainable in mixed coniferous forests that historically had high frequency/low severity fire regimes (Everett et al. 1995) and in Douglas-fir dominated forests that are succeeding toward climatic climax dominated by grand fir trees.

Reducing the risk of uncharacteristically intense wildfires in the relatively dry grand fir and Douglas-fir forests occupied by productive spotted owls should be of highest management priority. Thinning grand fir understory trees in Douglas-fir/grand fir forests should improve habitat for spotted owls, provided that overstory canopy cover exceeds 30%. However, in the Douglas-fir/ponderosa pine zone fire suppression and outdated partial-cutting practices led to increases in Douglas-fir thickets, which ostensibly allowed spotted owls to colonize previously sparse ponderosa pine stands that probably did not harbor spotted owls historically. There, reducing densities of Douglas-fir trees and ground-level fuel loads via extensive thinning of relatively small-diameter trees (13-40 cm dbh) could conceivably have a detrimental effect on owl reproductive success or occupancy. Judicious partial-cutting could create new foraging habitat for spotted owls by creating small-gap openings in large, dense forest stands by promoting understory shrubs (Oliver et al. 1994, Carey and Wilson 2001), particularly near riparian zones. Hayward (1997) noted that experimental timber harvest activities that maintain structural components of late-successional forest, well-dispersed across landscapes, may be compatible with conservation of boreal owls (*Aegolius funereus*). Similar adaptive management and monitoring will be required to develop silvicultural practices that are compatible with northern spotted owls (Irwin and Wigley 1993) and sustainable forest management along the eastern slope of the Cascades Mountains.

Conservation reserves for spotted owls are based largely upon applications of conservation-biology theory and univariate analyses of habitat selection, such that the most preferred successional stages (i.e., LSF) are now protected (e.g., Thomas et al. 1990). Hobbs and Hanley (1990) encouraged habitat selection studies to clarify influences of apparently preferred habitat conditions on population performance. We found that population performance among spotted owls was influenced by physical environmental factors that also influenced habitat selection at the landscape level. Thus, we encourage applying abiotic criteria in addition to seral-stage associations for assessing habitat in planning conservation strategies for priority species such as northern spotted owls. Mapping the preferred successional stages (i.e., LSF) from habitat selection studies and including territories known to be occupied by owl pairs (i.e., Thomas et al., 1990) represented a reasonable place to begin. Yet LSF does not sufficiently incorporate the complex set of interacting factors that influence spotted owl territory selection and population performance.

Regardless of the impacts of silvicultural treatments to restore forest sustainability in this region, we question the wisdom of predicating conservation for northern spotted owls solely upon old-growth forests. In our study area, reliance on LSF maps resulted in identifying some LSRs in poor-quality locations (e.g., glaciated landtypes) where subpopulations of spotted owls probably exist as reproduction sinks (Irwin and Wigley 1993). Reproduction sinks are areas where pairs persist but are unable to produce sufficient young to maintain population size. Prudence dictates identifying source areas, or those where owl pairs demonstrate potential for sustained reproduction and survival. However, we have yet to evaluate rates of survival relative to vegetation conditions, FMAZ or physical environmental factors. It is possible that locations where owls are most productive may differ from those where survival is high, as Franklin et al. (2000) observed in northwestern California.

Yet, even calculating survival rate may be insufficient: Watkinson and Sutherland (1995) noted that it is almost impossible to identify sources and sinks simply from demographic measures of birth and death rates. And Raphael et al. (1996) noted that interpretations from demographic data may be complicated when combining estimates from heterogeneous subpopulations consisting of mixtures of sources and sinks. These complications happen because demographic rates may be influenced by density dependence relative to immigration and emigration of juveniles and because estimates of population trends are determined by the relative proportions of source and sink territories in an area.

Significantly reducing LSF around owl territories through intensive timber harvesting would ultimately reduce reproductive success and cause further territory abandonment. Thus, natural resource management agencies have promulgated guidelines that specify prudent levels of timber harvesting. However, our data do not allow identification of such thresholds in each forest type along the eastern slope of the Cascade Mountains. The territories where owls exhibited the highest rates of reproduction actually contained 25% *less* LSF within a 3.4-km radius than at locations where owl pairs exhibited the lowest rates of reproduction. And we note that territory abandonment is occurring in the absence of forestry, implying that successional dynamics, competition from barred owls, weather, insect-caused defoliation, or some combination thereof could be causes. Our information does suggest that guidelines for protecting spotted owls while allowing careful restorative silvicultural activities should vary among the FMAZs until more detailed information is available. Long term adaptive management and monitoring experiments would appear to provide the optimal means of clarifying the complex relationships and restoring sustainable spotted owl populations and forests. Ultimately, we suggest that federal agencies move from narrowly-focused, species-dominated forest management strategies to a landscape-ecosystem approach (Drennan and Beier 2003) that reflects a variety of resources in concert with natural disturbance regimes and inherent productivity, as suggested by Huston (1999).

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