Barred Owls and Forest Fragmentation in Oregon Coast Range Spotted Owl Sites

by

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ABSTRACT.- Little information is available on northern barred owl (*Strix varia varia*) life history in the Pacific Northwest but their invasion into northern spotted owl habitat (*Strix occidentalis caurina*) appears to be significant and detrimental to conservation of the latter species. Forest fragmentation has been suggested as a possible factor in barred owl expansion and competitive advantage over spotted owls but until now, this hypothesis has not been evaluated. Forest fragmentation, elevation, and distance to water was measured in 60 spotted owl nest sites in the Siuslaw National Forest using satellite imagery and a Geographic Information System (GIS). Comparisons were made between sites with and without barred owl detection within 0.8 km and between sites with and without spotted owl displacement by barred owls. Comparison of forest fragmentation between owl sites and 74 random sites within the study area were also made to evaluate performance of the methodology. Total habitat and mean nearest-neighbor distance to habitat were the metrics used to estimate forest fragmentation. Measurements were made in 400, 800, and 1600-meter radius plots around each owl site to investigate effects of scale. Logistic regression was used to draw inferences on the effect of forest fragmentation, elevation, and distance to water on the odds of barred owl detection and spotted owl displacement. These variables were found to have no effect on the odds of detection and displacement in all three plot sizes. This suggests that macro-habitat resource partitioning is not yet occurring and this has implications for the long-term survival of the northern spotted owl.

Introduction

The range expansion of the northern barred owl (*Strix varia varia*) into northern spotted owl (*Strix occidentalis caurina*) habitat during the last four decades has caused considerable concern and interest among regional land managers and researchers (Taylor and Forsman 1976, Hamer 1988, Sharp 1989, Dunbar et al. 1991, Dark et al. 1998, Kelly 2002). Conservation efforts for the northern spotted owl have focused on loss of habitat, yet competition between the two congeners has been recognized as a potentially important force in northern spotted owl population decline (Thomas et al. 1990, Dunbar et al. 1991, Dark et al. 1998, Forsman *in* Welch 2000). Barred owls are larger, and aggression towards spotted owls has been frequently observed (Hamer et al. 1989, Dark et al. 1998, Leskiw and Gutierrez 1998). Diet and habitat preferences appear to overlap significantly where the two species are sympatric, providing the driving force for this competition (Hamer 1988). Documentation of northern spotted owl displacement by barred owls is sparse but believed to be occurring frequently throughout the range (Hamer et al. 1989, Dunbar et al. 1991, Dark et al. 1998, Kelly 2002). A recent review of data from several study sites in Oregon and Washington found that northern spotted owl site occupancy declined significantly after barred owls were detected within 0.8 kilometers of site centers (Kelly 2002). Over 25 cases of adult hybrids and an equal number of juvenile hybrids have been documented and this has also raised concern for the long-term viability of the northern spotted owl as a species (Hamer et al. 1994, Kelly 2002).

In terms of rate and extent, the barred owl expansion into the northwest has been one of the most impressive of any avian expansions during the last century (Johnson 1994). Barred owls were historically associated with deciduous and coniferous forests east of the Great Plains and have moved across Canada and down into Washington, Oregon, and northern California beginning in the 1940's (Taylor and Forsman 1976, Johnsgaard 1988, Dunbar et al. 1991). Since the first Oregon state record in 1974, barred owls have become abundant in many western Oregon forests (Kelly 2002). In the Siuslaw National Forest (SNF), for example, barred owl detections at northern spotted owl sites increased 10-fold in 10 years between 1990 and 1999 (data from Kelly 2002). As of 1987, no barred owl detections were made at SNF spotted owl sites, but by 1999, barred owls had been found in one third of all SNF spotted owl territories (Kelly 2002). In California, barred owls are believed to have arrived in the early 1980's and the population rapidly increased during the next two decades (Dark et al. 1998). Barred owl expansion has apparently followed a similar pattern in the Rocky Mountains, with estimated arrival in northern Idaho in the early 1980's and a rapid increase in subsequent years (Wright and Hayward 1998).

Despite recognition as a significant phenomenon, the causes and implications of barred owl expansion into the Pacific Northwest are poorly understood. Decades of clear-cut logging and the resulting fragmentation of western forests have been frequently suggested as important factors facilitating barred owl expansion and the apparent displacement of spotted owls, however, this hypothesis has not been adequately tested (Hamer 1988, Hejl 1994, Root and Weckstein 1994, Dark et al. 1998). Two studies have shown a possible correlation between barred owl presence and fragmentation in the

Pacific Northwest (Hamer 1988, Herter and Hicks 2000). Hamer (1988) found that barred owls occurred more frequently in heavily logged landscapes in northern Washington. This study also indicated that barred owls had much smaller home range requirements and much broader diets than spotted owls. These two life history characteristics may enable barred owls to be less sensitive to habitat fragmentation. A more recent study examined habitat characteristics at barred owl and spotted owl locations in the central Washington Cascades and found that barred owl sites contained less old growth forest habitat than spotted owl sites (Herter and Hicks 2000). Based on these studies, one would predict that a relationship between habitat fragmentation and barred owl presence might indeed exist.

Questions remain, however, because considerable anecdotal evidence suggests that barred owls can occupy large contiguous stands of old growth forest as readily as fragmented landscapes in the Pacific Northwest (Dark et al. 1998, Dunbar 1991, Wright and Hayward 1998). In the eastern portion of their range, barred owls are strongly associated with contiguous old-forest and wooded riparian stands (Johnsgaard 1988, Laidig and Dobkin 1995, Haney 1997, Mazur et al. 1998). Examination of barred owl expansion into the northern Rocky Mountains has also shown that the species can occupy large tracts of forested wilderness (Wright and Hayward 1998). The relationship between habitat fragmentation and barred owl expansion within the range of the northern spotted owl has not been sufficiently investigated. The potential impacts of barred owl expansion on spotted owl population recovery make this an even more interesting and salient direction for research.

In an effort to contribute new insight into the issue, this study examined the relationship between forest fragmentation and barred owl detections at SNF northern spotted owl sites in the Oregon Coast Range. Several broad ecological questions were of particular interest and provided a conceptual framework for this study. Has forest fragmentation facilitated barred owl range expansion in the region? Are barred owls better able to survive and reproduce in fragmented forest than spotted owls? Are spotted owls better able to compete and hold territory in less fragmented habitat? Have the two previously allopatric species begun a process of habitat partitioning in order to reduce competition? If answers to any of these questions are yes, one might expect that forest characteristics in spotted owl sites where barred owls are present would differ from spotted owl sites where barred owls are absent.

Based on these questions, I developed two hypotheses to test in this project: (1) the odds of barred owl detection within 0.8 kilometers of spotted owl sites increase with greater amounts of forest fragmentation, and (2) the odds of spotted owl displacement by barred owls increase with forest fragmentation. Forest fragmentation was measured in four hundred, 800, and 1600-meter radius plots (54, 207, and 818 hectares) around spotted owl sites. Different plot sizes were used to improve the study's sensitivity to biologically relevant effects of scale. Studies comparing spotted owl sites and random sites have consistently shown habitat characteristics to be important out to 800 meters from site centers with decreasing importance beyond 1600 meters (Hunter et al. 1995, Meyer et al. 1998, Swindle et al. 1999). I tested whether existing landcover data are consistent with this relationship in the SNF as well by comparing spotted owl sites against a group of randomly selected sites.

In addition to forest fragmentation, distance to water and elevation were also included as variables of interest. Distance to water was included because of the importance of riparian habitat for barred owls in the eastern portion of their range (Johnsgard 1988). It is not known if barred owls select for riparian forest in the Pacific Northwest. Elevation was included in analysis because it has been suggested as a possible influence by the two previously cited barred owl studies from Washington (Hamer et al. 1989, Herter and Hicks 2000). Both of those studies found that barred owls were more common at lower elevations. Barred owls are also reported to occur more frequently at lower elevations than spotted owls in California (Dark et al. 1998).

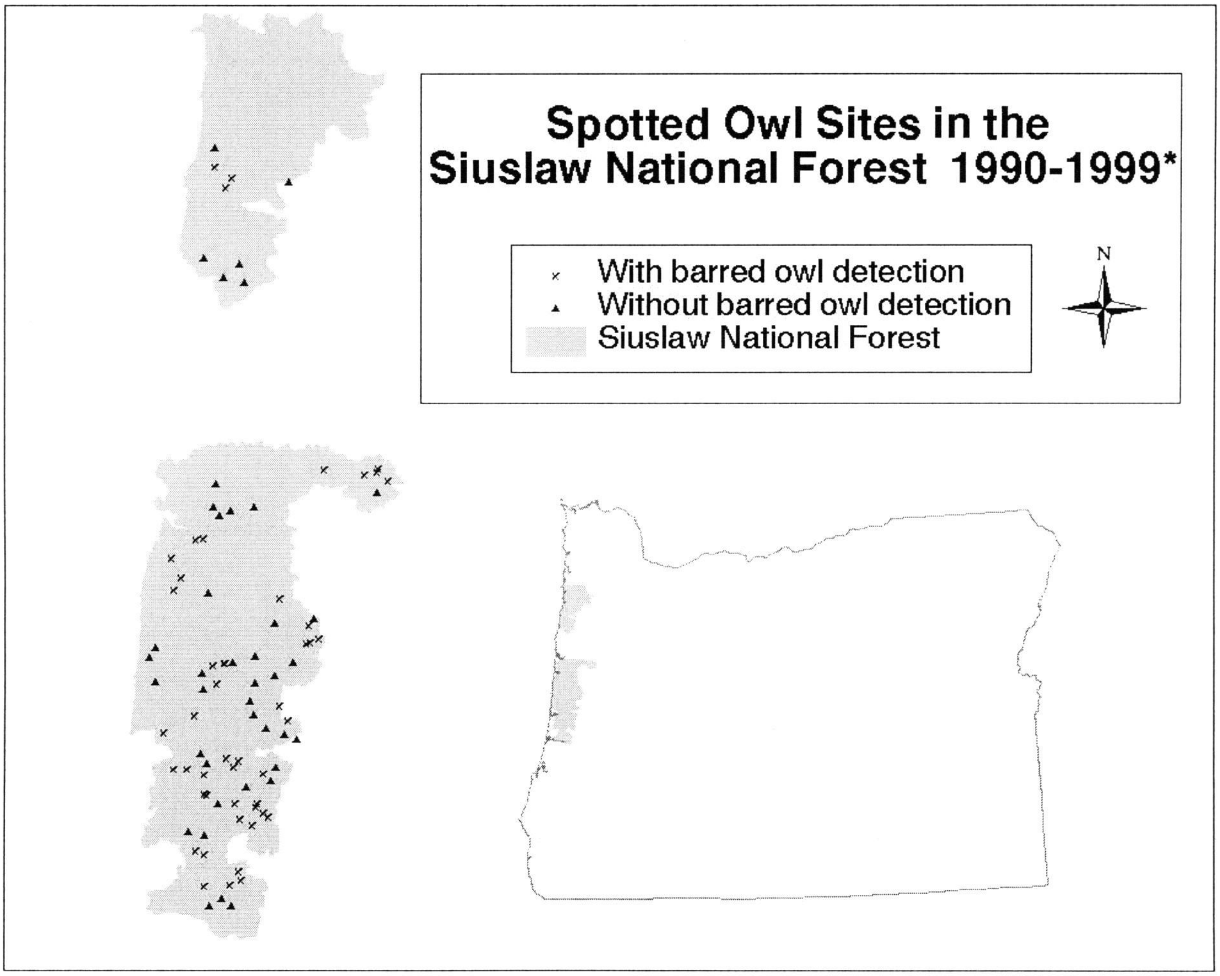
Analysis was restricted to a comparison of spotted owl sites with and without barred owl detections rather than between separate spotted owl and barred owl sites. This restriction was driven by two important considerations. First, all barred owl data in the northwest has been collected via spotted owl surveys in which barred owl responses to spotted owl vocalizations were recorded but rarely investigated further (excepting Hamer 1988), thereby limiting our ability to identify barred owl activity centers. Second, barred owls in the northwest occur across a much broader range of forest conditions than spotted owls (Kelly 2002). Comparisons between separate groups of barred owl and spotted owl sites will tend to reflect only the broader habitat tolerances of barred owls rather than any important differences in spotted owl habitat that increase susceptibility to barred owl invasion. Thus, comparing spotted owl sites with and without barred owl detections allows for more direct inference to influences of environment on spotted owl habitat and is of more interest within the context of spotted owl conservation. This design is especially important for detecting possible resource partitioning and conditions under which differences in competitive advantage may exist.

Study Area

The Siuslaw National Forest (SNF) served as the project study area. The SNF is located in the central Oregon Coast Range and contains approximately 3,000 km^2 of forestland (See fig. 1). The region is topographically mature and is notable for its deeply dissected landscape (Franklin and Dyrness 1988). Elevations range from sea level to 1241 meters. The SNF is dominated by the mild maritime climate characteristic of Pacific Northwest coastal regions. Annual precipitation averages approximately 200 cm, over half of which falls between October and January (Anderson et al. 1998). Temperatures are relatively mild throughout the study area. Twenty-year average January minimum and July maximum temperatures from the Newport, Oregon weather station are 37°F and 64°F, respectively (OCS 2002).

Two major vegetation zones occur in the study area and both zones provide suitable spotted owl habitat (Franklin and Dyrness 1988). The Sitka spruce (*Picea sitchensis*) vegetation zone occurs along the coastal portions of the study area and extends inland along river valleys. The western hemlock (*Tsuga heterophylla*) vegetation zone occurs throughout the interior portion of the study area. Grassy balds and subalpine vegetation occur as minor components on the higher peaks. Dominant overstory species include Douglas-fir (*Pseudotsuga menzeisii*), western red cedar (*Thuja plicata*), and red alder (*Alnus rubra*). Red alder primarily occurs along riparian areas, but can dominate stands

Fig. 1. The location of the Siuslaw National Forest study area in Oregon and the distribution of spotted owl sites used in the study. *This figure represents the 99 sites used in this study and does not include all spotted owl sites in the Siuslaw National Forest between 1990-1999.



that have been recently harvested or burned. Major components of the forest understory include vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and sword fern (*Polystichum munitum*) (Franklin and Dyrness 1988).

Timber production was the primary management goal in the SNF for most of the last century and some of the most productive forestland in the world occurs there. Commercial logging began in the 1930's and continued until the spotted owl related court injunctions of the late 1980's. Extensive clear-cutting has created a highly fragmented landscape, which has significantly impacted northern spotted owl populations (Forsman et al. 1996). Demographic analysis for the SNF spotted owl population indicated that it was experiencing significant decline, possibly as much as 12% annually, between 1990 and 1993 (Forsman et al. 1996). With the federal listing of the northern spotted owl as a threatened species in 1990, the SNF experienced a dramatic reorganization of management objectives and very little timber harvest has occurred there since 1990 (Forsman et al. 1996). Meta-analysis conducted in 1999 showed that while northern spotted owl populations throughout Washington, Oregon, and Northern California continue to decline at an estimated 3.9% annually, declines in SNF populations appear to be less steep (Franklin et al. 1999).

Barred owl records for Oregon and Washington indicate that the species did not arrive in the SNF until rather late in the sequence of expansion (Kelly 2002). Numerous reports exist for the Oregon Cascades and southern Oregon coast range during the early 1980's and barred owls were reported in Northern California as early as 1981 (Dark et al. 1998, Kelly 2002). However, the first report for the SNF was not until 1990 (Kelly 2002). This same pattern occurred in Washington, where barred owls had moved throughout the

Washington Cascades during the 1970's but did not appear on the Olympic Peninsula until 1985 (Sharp 1989). This suggests that barred owls may have moved south down the Cascades and then moved west and north back up the coast range. The annual sequence of barred owl detections at spotted owl sites in the SNF shows a similar northward trend (data from Kelly 2002). Figure 2 shows three maps of the study area showing spotted owl sites with barred owl detections for 1990, 1995, and 1999. A trend of occurrences increasing from south to north is clearly discernible in this figure, as is a dramatic increase in the number of barred owl detections. Between 1990 and 1999, barred owl detections increased 10-fold in the study area. Although the SNF did not formally become a long-term demographic study area until 1990, it is important to note that survey efforts in the Oregon Coast Range and the SNF, in particular, had been ongoing throughout the 1980's. It is generally believed that the increase in barred owl detections in the SNF during the 1990's was not a result of increased survey effort (E. Forsman pers. comm.). A similar conclusion was reached in a review of the barred owl expansion in northern California as well (Dark et al. 1998).

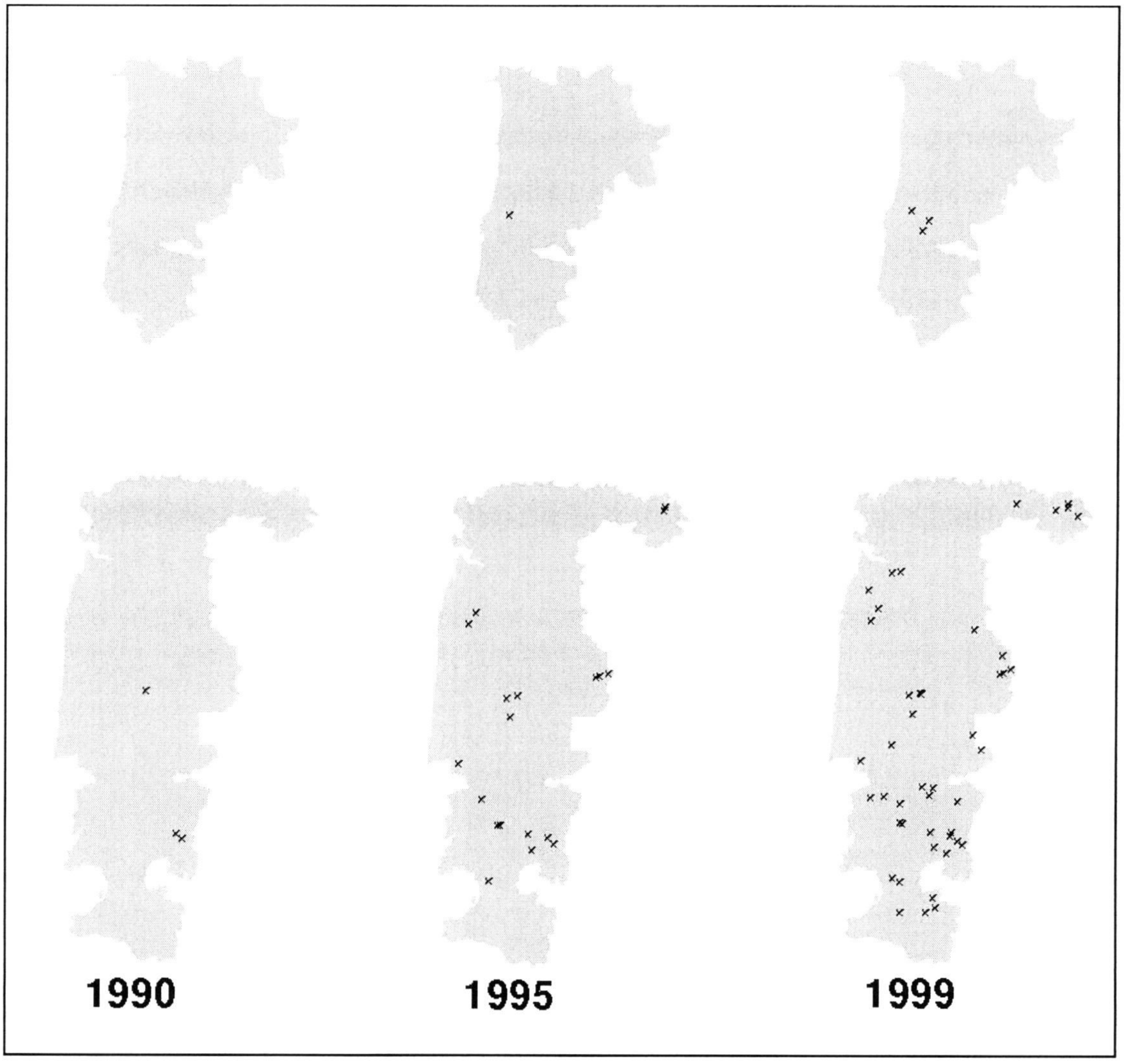


Fig. 2. Spotted owl sites with barred owl detections in the Siuslaw National Forest, Oregon as of 1990, 1995, and 1999.

Methods

A combination of commercial GIS software packages were used to measure habitat fragmentation in 400, 800, and 1600-meter radius plots (54, 207, and 818 hectares, respectively), as well as owl site distance to water and site elevation. Logistic regression was used to make statistical inferences about the relationship of barred owl detection and spotted owl displacement to fragmentation and topographic covariates. Because spotted owl habitat association is well described and predictable, a comparison of spotted owl sites and random sites were used in order to assess the performance of the study methods. Since no direct measure of forest fragmentation exists, it was estimated with two different metrics; total habitat and a fragmentation index developed by Ripple et al. (1991b). These metrics were measured at each owl site for all plot sizes. Total habitat was determined by calculating the total number of habitat pixels in each plot and converting to total hectares of habitat. Low total habitat values were interpreted to indicate a more fragmented landscape.

The fragmentation index was determined by calculating the mean distance, in meters, of each non-habitat pixel from the nearest habitat pixel. A high fragmentation index value was interpreted to indicate a more fragmented landscape. This metric has been useful in previous studies of spotted owl habitat (i.e. Ripple et al. 1991a, 1997, Hunter et al. 1995). Because habitat amount, habitat patch size, and inter-patch distance are strongly correlated, the fragmentation index is a good indicator of landscape pattern. For example, a reduction in habitat amount requires either a reduction in patch size or an increase in inter-patch distance, which results in a more fragmented landscape (Harrison and Fahrig 1995). This relationship enables the representation of multiple landscape pattern characteristics by a single parameter.

Spotted owl activity centers - Federal employees conducted spotted owl surveys during a 10-year period from 1990 to 1999 to determine spotted owl occupancy, reproductive status, and site center locations. Standard survey protocols were followed (Franklin et. al 1996). Barred owl detections and locations were recorded during these surveys. Kelly (2002) reviewed the SNF survey data to determine barred owl detections within 0.8 kilometers of site centers and provided a list of sites for this study. Each site included in this study had at least 5 years of complete survey data. A final list of 99 sites suitable for analysis was assembled based on this criterion. Forty of these 99 sites had barred owl detections made within 0.8 kilometers of the site center in one or more years during the study period. Sixty sites were randomly selected from the final list for analysis, of which 23 sites had barred owl detections.

Spotted owl displacement was analyzed separately from detection, and sites that met the following conditions were considered to have experienced displacement: (1) sites were occupied by spotted owls at least 2 years prior to barred owl detection and not occupied by spotted owls during the first year following barred owl occupation, or (2) sites had 2 or more years of barred owl detection through 1999. Sixteen sites of the 99 total sites met these criteria. Random selection of 60 sites used in this analysis included 9 sites with displacement.

Habitat Classification - An owl habitat map for the entire study area was developed from the 1996 vegetation GRID coverage developed by Ohmann (2000a). This coverage was created through classification of 1996 25-meter pixel Landsat TM imagery.

Classification was done using a gradient nearest neighbor method (see Ohmann 2000b). A total of 13 land cover classes were used. Classification accuracy for individual land cover classes ranged from 79-94% (Ohmann 2000a). Overall classification accuracy of the image was 88% (Ohmann 2000a).

The image was reclassified into habitat and nonhabitat land cover classes. The habitat definition used in this study followed several previous spotted owl habitat studies (Hunter et al. 1995, Ripple et al. 1997, Swindle et al. 1999). The habitat class included all forest classes with > 1.4 m^2/ha basal area with trees $\geq$ 50 cm dbh. All other classes were assigned to nonhabitat. The image was filtered using the CLUMP and SEIVE procedures in ERDAS Imagine (ERDAS, Inc. 1997 vers. 8.3) to remove all habitat clumps less than 8 pixels (0.5 ha). This was done to eliminate some classification error (salt and pepper effect) and to establish a minimum habitat patch size. The determination of a minimum patch size is not well described in the literature. The decision to use a 0.5-hectare minimum size was somewhat subjective and based on personal field experience and procedures used by Swindle et al. (1999).

Habitat Analysis - 400, 800, and 1600-meter radius circular plots were created around each site center and overlaid on the habitat map. The EXTRACT procedure in Idrisi32 (Clark Labs 1999) was used to obtain the sum of all habitat pixels within each plot. The sum of all pixels was converted to hectares to produce the total habitat metric. The fragmentation index was developed with the DISTANCE procedure in Idrisi32 and owl site plots were overlaid on top of this output. EXTRACT was used to obtain the mean distance for each plot. Fragmentation index values were calculated in meters. Distance to water was calculated by using the DISTANCE procedure on a stream coverage originating from a 10-meter digital elevation model (DEM) (Miller et al. 2001). The stream coverage was reclassified to include only 3rd to 7th order streams. This decision was based on the high degree of precision obtained from the 10-meter DEM and the deeply dissected coastal mountain terrain. Riparian influences relevant to barred owls are marginal along the small and ephemeral 1st and 2nd order streams in this region. Distance to water was calculated for site centers rather than summarized for the circle plots. A mosaic of 30-meter DEMs of the study area was used to calculate site elevation (Christiansen 2001). Both distance to water and elevation are calculated in meters.

Statistical Analysis - Two logistic regression models were developed for the study. The first model tested the odds of barred owl detection within 0.8 kilometers of spotted owl sites as a function of forest fragmentation at 400, 800, and 1600 meters from site centers, as well as site distance to water and site elevation. A binary response variable was constructed by assigning a value of 1 to sites with detections and a value of 0 to sites without detections. In the logit function, the dependent variable was the natural log (ln) of the odds of barred owl detection [logit(π_b), where π_b is the probability of barred owl detection]. A second logistic regression model tested the odds of spotted owl displacement by barred owls as a function of the same set of explanatory variables. In this model the binary response was developed by assigning a value of 1 to sites experiencing displacement and a value of 0 to sites not experiencing displacement. The dependent variable for this logit function was the natural log of the odds of spotted owl displacement as the logit(π_d), where π_d is the probability of spotted owl displacement.

Ramsey et al. (1994) showed the significant influence of overlapping circle plots and subsequent correlation in estimating model parameters in similar studies of spotted owl sites and random sites. Thus, separate equations were constructed for each plot size in this study. Exploratory analysis also indicated that total habitat and fragmentation index were significantly correlated ($r \leq -75$). Separate equations were used for each fragmentation metric to avoid this problem.

The following generalized linear model was used: $\text{logit}(\pi) = \beta_0 + \beta_1(\text{Habitat}_x) + \beta_2(\text{Dist. to Water}) + \beta_3(\text{Elevation})$, where x is the plot size (i.e. 400 meters), "Habitat" is total habitat (or "Frag. Index", which represents fragmentation index), and "Dist. to Water" is site distance to water. Model selection was accomplished using the Bayesian information criterion (BIC) (Ramsey and Schaffer 1997). BIC values were obtained using the formula: $\text{BIC} = \text{Deviance} + [p^*\ln(n)]$, where p is the number of parameters and n is the sample size (Ramsey and Schaffer 1997). This procedure is used to select a model with the smallest BIC value from a subset of all possible models. The BIC procedure rewards simple models with fewer explanatory variables. This emphasis in parsimony is a highly desirable feature of the BIC procedure for studies such as these in which errors of commission are of greater concern than errors of omission (Ramsey and Schaffer 1997, Murtaugh 1998). Whereas inclusion of too many covariates increases the likelihood of detecting spurious significant differences, use of the BIC is conservative and tends to err on the side of caution. Backward elimination of least significant variables was used to reduce the total number of models considered in BIC procedures. Wald's tests were used to assess whether individual logistic regression coefficients differed significantly from 0 (Ramsey and Schaffer 1997).

Random Sites - While the positive relationship between the amount and distribution of old growth forest and spotted owls has been documented in numerous studies throughout the species' range (i.e. Swindle et al. 1999), no studies have been done for the SNF. In order to confirm that this relationship was consistent for the SNF, total habitat and the fragmentation index were compared between spotted owl sites and random sites. This also provided an opportunity to assess the ability of the techniques used in this study to detect a real biological "signal" from background "noise". One-hundred random locations were generated within the study area boundary for comparison with 60 spotted owl points using the random point generator feature of the ALASKA PAK extension for ArcView (NPS 2001). Sixteen-hundred-meter radius plots were created around these points and sites that overlapped with the 1600-meter radius owl site plots were discarded. Seventy-four random sites remained after this procedure. Comparison of fragmentation metrics between owl sites and random sites followed the methods described above. No comparison of elevation and distance to water between random and owl sites was made and there is no indication from the literature that these are useful predictors.

Results

Barred Owl Detection - The odds of barred owl detection in spotted owl sites were not significantly associated with total habitat in the SNF. The effect of variable plot sizes at 400, 800, and 1600-meter radii also was not statistically significant. Table 1 shows the mean values of the explanatory variables for sites with and without barred owl detection for each plot. The amount of habitat was greater in sites without barred owl detections, as hypothesized, however these differences were small. Differences in the mean number of hectares were greatest at 1600-meter radius plots, where sites without barred owl detections were estimated to contain an average of 55 more hectares of habitat than sites with barred owl detection. The results of model selection indicated that the model with total habitat at 1600-meter radius plots was most preferable (Table 2).

Table 1. Summary statistics of explanatory variables for northern spotted owl sites with and without barred owl detection in the Siuslaw National Forest, 1990-1999.

	With Detection (n=23)		Without Detection (n=37)	
Variable	Mean	SD	Mean	SD
$Habitat_{400}$ (ha)	32	12	35	11
Frag. $Index_{400}$ (m)	29	40	24	29
$Habitat_{800}$ (ha)	106	31	119	42
Frag. $Index_{800}$ (m)	39	29	37	39
$Habitat_{1600}$ (ha)	356	113	412	142
Frag. $Index_{1600}$ (m)	58	36	54	64
Elevation (m)	208	76	238	93
Dist. to Water (m)	447	365	395	272

Table 2. Results of BIC model selection for the odds of barred owl detection in the Siuslaw National Forest, 1990-1999.

Model	BIC
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{1600})$	85.53
$logit(\pi_b) = \beta_0+\beta_1(Elevation)$	86.30
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{800})$	86.37
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{400})$	87.29
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{1600})+ \beta_2(Elevation)$	87.66
$logit(\pi_b) = \beta_0+\beta_1(Dist.Water)$	87.67
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{400})$	87.79
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{1600})$	87.98
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{800})$	88.05
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{800})+ \beta_2(Elevation)$	88.39
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{400})+ \beta_2(Elevation)$	89.62
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{1600})+ \beta_2(Elevation)$	90.20
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{400})+ \beta_2(Elevation)$	90.28
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{800})+ \beta_2(Elevation)$	90.36
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{1600})+ \beta_2(Dist.Water)+ \beta_3(Elevation)$	91.33
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{800})+ \beta_2(Dist.Water)+ \beta_3(Elevation)$	91.87
$logit(\pi_b) = \beta_0+\beta_1(Habitat_{400})+ \beta_2(Dist.Water)+ \beta_3(elevation)$	92.21
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{800})+ \beta_2(Dist.Water)+ \beta_3(Elevation)$	92.42
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{1600})+ \beta_2(Dist.Water)+ \beta_3(Elevation)$	92.58
$logit(\pi_b) = \beta_0+\beta_1(Frag\ Index_{400})+ \beta_2(Dist.Water)+ \beta_3(Elevation)$	92.64

Table 3. Results of logistic regression for single variable models: logit $(\pi_b) = \beta_0+\beta_1(x)$, intercepts are not included. There was no effect of fragmentation and topography on the odds of barred owl detection.

Explanatory Variable	Coefficient	SE	Z-Statistic	P-Value
$Habitat_{400}$	-0.020	0.022	-0.88	0.37
$Frag.\ Index_{400}$	0.004	0.007	0.52	0.60
$Habitat_{800}$	-0.009	0.007	-1.28	0.20
$Frag.\ Index_{800}$	0.001	0.007	0.13	0.89
$Habitat_{1600}$	-0.003	0.002	-1.55	0.12
$Frag.\ Index_{1600}$	0.001	0.004	0.29	0.77
Elevation	-0.004	0.003	-1.28	0.20
Dist. To Water	0.001	0.001	0.63	0.53

Logistic regression results for the model $\text{logit}(\pi_b) = \beta_0+\beta_1(\text{Habitat}_{1600})$ showed that total habitat did not influence the odds of barred owl detection (2-sided p-value = 0.12). Table 3 shows the results of logistic regression for the total habitat variable at all 3 plot sizes. The fragmentation index, which measured the mean distance between patches of habitat, had no effect on the odds of barred owl detection in the SNF. As hypothesized, the mean fragmentation index values were consistently greater in all plot sizes at sites with barred owl detection, however the differences were very small. Mean differences at each plot size ranged from less than 1 meter to about 4 meters. BIC values were higher than models with total habitat (see table 2) and results of logistic regression indicated that the fragmentation index had no influence on the odds of barred owl detection at any plot size (2-sided p-values $\geq$ 0.6; see table 3).

No association between either site distance to water or elevation and the odds of barred owl detection was found in the SNF (2-sided p-values = 0.53 and 0.20, respectively). Table 1 shows the mean values for sites with and without barred owl detection. Sites with detection on average occurred at slightly lower elevations and were approximately 50 meters farther from water than sites without barred owl detection. However, the inclusion of these variables in the regression models did not significantly lower residual deviance or BIC values (see table 2).

Spotted Owl Displacement - Results from logistic regression for the odds of spotted owl displacement in the SNF were similar to those of barred owl detection. BIC model selection results suggested that the model $\text{logit}(\pi_d) = \beta_0+\beta_1(\text{Habitat}_{1600})$ was preferable (see table 4). No association was found between the mean number of habitat hectares at 1600-meter radius plots and the odds of spotted owl displacement by barred owls in the

SNF (2-sided p-value = 0.12). Table 5 shows the mean values for total habitat at all 3 plot sizes. Total habitat was consistently greater in sites without displacement, but as with barred owl detection, was not significant when included in logistic regression equations (see table 6). Differences were greatest in the 1600-meter plots, where sites without displacement had an average of 72 hectares of habitat more than sites with displacement.

Table 4. Results of BIC model selection for models of the odds of spotted owl displacement in the Siuslaw National Forest, 1990-1999.

Model	BIC
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{1600})$	56.33
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{800})$	57.13
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Dist.Water})$	57.40
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{800})$	57.90
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{400})$	58.36
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{1600})$	58.37
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Elevation})$	58.85
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{400})$	58.87
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{1600}) + \beta_2(\text{Dist.Water})$	60.13
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{800}) + \beta_2(\text{Dist.Water})$	60.74
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag}_{400}) + \beta_2(\text{Dist.Water})$	60.97
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{800}) + \beta_2(\text{Dist.Water})$	61.21
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{1600}) + \beta_2(\text{Dist.Water})$	61.46
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Hab}_{400}) + \beta_2(\text{Dist.Water})$	61.48
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{1600}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	63.43
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{800}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	63.79
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{400}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	64.03
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{800}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	64.27
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Frag Index}_{1600}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	64.27
$\text{logit}(\pi_b) = \beta_0 + \beta_1(\text{Habitat}_{400}) + \beta_2(\text{Dist.Water}) + \beta_3(\text{Elevation})$	64.30

Table 5. Summary statistics of explanatory variables for northern spotted owl sites with and without displacement by barred owls in the Siuslaw National Forest, 1990-1999.

	With Displacement (n=9)		Without Displacement (n=51)	
Variable	Mean	SD	Mean	SD
$Habitat_{400}$ (ha)	32	15	33	12
Frag. $Index_{400}$ (m)	37	61	28	29
$Habitat_{800}$ (ha)	96	39	114	38
Frag. $Index_{800}$ (m)	38	35	51	40
$Habitat_{1600}$ (ha)	316	108	389	126
Frag. $Index_{1600}$ (m)	72	37	57	56
Elevation (m)	231	87	241	120
Dist. to Water (m)	563	370	401	343

Table 6. Results of logistic regression for single variable models: $logit(\pi_b) = \beta_0+\beta_1(x)$, intercepts are not included. There was no effect of fragmentation and topography on the odds of spotted owl displacement.

Explanatory Variable	Coefficient	SE	Z-Statistic	P-Value
$Habitat_{400}$	-0.005	0.029	-0.18	0.85
Frag. $Index_{400}$	0.006	0.008	0.76	0.44
$Habitat_{800}$	-0.012	0.009	-1.31	0.19
Frag. $Index_{800}$	0.009	0.008	1.03	0.30
$Habitat_{1600}$	-0.004	0.002	-1.57	0.12
Frag. $Index_{1600}$	0.004	0.005	0.77	0.44
Elevation	-0.001	0.003	-0.24	0.20
Dist to Water	0.001	0.001	1.25	0.21

Fragmentation index values had no effect on the odds of spotted owl displacement at any plot size (2-sided p-values ≥ 0.2). Again, fragmentation index values were consistently greater in sites with spotted owl displacement (except for Frag. $Index_{800}$) but the differences were not statistically significant. Differences in mean values ranged from 10 to 15 meters. Distance to water and elevation were also found to have no effect on the odds of spotted owl displacement in the SNF (2-sided p-values = 0.21 an 0.81 respectively). Sites with displacement were approximately 160 meters farther from water and 10 meters lower in elevation, but these differences were not statistically significant.

Random Sites - Differences in total habitat and fragmentation index between spotted owl sites and random points within the SNF study area were large and significant for all plot sizes (2-sided p-values < .001, t-test). Table 7 shows the magnitudes of the difference in means. The relationship between fragmentation index and total habitat was consistent in all plot sizes. The fragmentation index was significantly smaller in spotted owl sites and total habitat was significantly greater in spotted owl sites. The logistic regression model $\text{logit}(\pi_b) = \beta_0+\beta_1(x)$ was also fit with this data, where the odds of spotted owl occupancy (owl = 1, random = 0) was estimated as a function of fragmentation metrics in all plot sizes. Coefficient values were highly significant for all variables in all plot sizes (2-sided p-value < 0.001, Wald's test). Table 8 shows the estimated increase in odds of spotted owl site occupancy for a change in each fragmentation variable equal to the mean differences between owl sites and random sites. The amount and spatial arrangement of habitat had a strong effect on the odds of spotted owl occupancy for all plot sizes but the effect was greatest in the 400-meter radius plots. In the smallest plot size, sites were 9.5 times more likely to be occupied by spotted owls for every 98-meter decrease in the fragmentation index (mean distance to habitat). In the 1600-meter radius plots, a 70 meter decrease in the fragmentation index increased the odds of spotted owl occupancy by only 1.9 times. Likewise, spotted owl occupancy was 5 times more likely in sites with an 18-hectare increase in habitat in 400-meter radius plots, whereas a 116-hectare increase in 1600-meter radius plots increased the odds of occupancy by only 1.6 times.

Table 7. Means, standard deviation, and mean differences for spotted owl sites and random sites in the Siuslaw National Forest, 1990-1999.

Variable	Owl Sites (n=60)		Random Sites (n=74)		Mean Difference
	Mean	SD	Mean	SD	
$Habitat_{400}$ (ha)	35	12	17	14	18
Frag. $Index_{400}$ (m)	25	34	123	161	-98
$Habitat_{800}$ (ha)	116	41	66	46	50
Frag. $Index_{800}$ (m)	38	38	133	146	-95
$Habitat_{1600}$ (ha)	382	135	266	156	116
Frag. $Index_{1600}$ (m)	61	57	131	133	-70

Table 8. The increased odds of spotted owl occupancy as explanatory variables increase by the difference between means. The effect of fragmentation on the odds was greatest in 400 ha. plots.

Variable	$\overline{X}_{owl}-\overline{X}_{random}$ [a]	$\hat{w}_{owl}/\hat{w}_{random}$ [b]	95% CI
$Habitat_{400}$ (ha)	18	5.1	2.6-10.6
Frag. $Index_{400}$ (m)	-98	9.5	2.94-30.9
$Habitat_{800}$ (ha)	50	2.7	2.0-5.5
Frag. $Index_{800}$ (m)	-95	4.9	2.6-10.5
$Habitat_{1600}$ (ha)	116	1.6	1.4-2.0
Frag. $Index_{1600}$ (m)	-70	1.9	1.3-3.1

[a] $X_{owl}-X_{random}$ is the difference between means for owl sites and random sites.

[b] $\hat{w}_{owl}/\hat{w}_{random}$ is the odds ratio calculated as $\exp[\beta_1 * (X_{owl}-X_{random})]$.

Discussion

Neither the presence of barred owls in spotted owl territories nor the displacement of spotted owls by barred owls appear to be associated with forest fragmentation, elevation, or distance to water in the Siuslaw National Forest. While there were consistently greater amounts of old growth forest habitat in spotted owl sites without barred owl detection and spotted owl displacement, the differences were less than expected and not statistically significant. The fragmentation index was consistently less in sites without barred owl detection and spotted owl displacement, but this difference was also small and statistically insignificant. Elevation and site distance to water also had no effect on the odds of detection and displacement. The odds of barred owl invasion into any particular spotted owl territory in the SNF, therefore, appear to be unaffected by fragmentation, elevation, and distance to water. The results from the comparison of spotted owl sites and random sites in the SNF showed strong differences in forest fragmentation consistent with previous studies from other locations in the region (Hunter et al. 1995, Meyer et al. 1998, Swindle et al. 1999). The comparison with random sites demonstrated that the methods used in this study performed well and the fragmentation metrics were adequately sensitive to real differences in habitat across the study area. This provides additional confidence to the conclusion of no difference in forest fragmentation between sites with and without barred owls. The inability to reject null hypotheses can suggest inadequate statistical power and inconclusive results. Certainly an increase in the number of owl sites or an increase in the precision of fragmentation measurement may have improved parameter estimates. However, these results provide evidence that spotted owl sites with barred owl detection do not differ from sites without barred owls. Both the comparison with random sites and the considerable variation in barred owl habitat reported in the literature (i.e. Johnsgaard 1988, Wright and Hayward 1998, Kelly 2002) are consistent with this conclusion.

This conclusion differs markedly from the two studies of barred owl and spotted owl habitat in Washington (Hamer 1988, Herter and Hicks 2000). These studies reported that spotted owl sites contained more old growth than neighboring barred owl sites. There are several possible reasons for this discrepancy. The most important concerns the difference in study design. Those studies compared separate groups of barred and spotted owl sites while this study looked specifically for differences within spotted owl sites. It is also possible that fundamental differences in the relationship between habitat and barred owl expansion exist between study areas. The Washington studies were conducted in the north and eastern portions of the Cascades where greater segregation in habitat may occur as a result of a patchier, less homogenous landscape. In particular, moisture may be a greater limiting resource for barred owls in the Washington study areas, causing their distribution to be aggregated along valley bottoms where clear cutting has had greater impact (Hamer 1989, Herter and Hicks 2000). Finally, both Washington studies were conducted during the 1980's or early 1990's, which was still early in the period of expansion. This opens up the possibility that barred owls may have initially colonized fragmented forest before eventually expanding into more contiguous old growth. This temporal question is an important one and should be addressed in future research.

Barred owls clearly require mature, closed-canopy forest but there appears to be broad amplitude in tolerance for different mature forest types (Hamer 1988, Johnsgaard 1988, Haney 1997, Mazur et al. 1998). The relatively small home range requirements and generalist diet reported by Hamer (1988) in Washington may be key life history characteristics that enable individuals of the species to survive and reproduce in both fragmented and contiguous forest landscapes. In Oregon, barred owl home ranges may be even smaller, since Oregon spotted owl home ranges are considerably smaller than those in Washington (Forsman et al. 1984, Hamer 1989). In the SNF, this plasticity in habitat selection by barred owls has resulted in complete spatial overlap with spotted owls. The results from this study indicate not only that barred owls will use fragmented and contiguous spotted owl territories with equal probability, but also that spotted owls are not better able to compete and hold territory in contiguous forest. This has important implications for the ecology of the two species and for the long-term survival of spotted owls.

From an evolutionary perspective, interspecific competition is considered mutually detrimental to the competing organisms and has only two possible outcomes: coexistence (via resource partitioning, hybridization, or speciation) or extinction (MacArthur 1972). As a result, it is more common to observe the outcome of historic competition rather than actual competitive interaction. Range expansion is one source of exception to this generality. The rapid expansion of the barred owl into the range of the northern spotted owl is a unique biogeographical event and provides an unusual opportunity to witness competition in progress (Brown and Lomolino 1998). The barred owl expansion is particularly interesting because it blurs the lines between “native” and “exotic” species. Most range expansions that involve competition and displacement involve “exotic” species that have moved as a result of human disturbance across historically impassable barriers such as oceans (Cox and Moore 2000). The role of human disturbance and the native/exotic designation for the barred owl case is not clear.

The incidence of relatively few cases of hybridization and the intensity of aggressive interactions between the two *Strix* owls indicates their short history of overlap (Hamer 1988, Hamer et al. 1994, Dark et al. 1998, Kelly 2002). It has been suggested that spotted owls and barred owls may have once been a superspecies and we may now be witnessing its reforming (Mayr and Short 1970). However, the rate of hybridization remains low relative to the scale of overlap now existing in the SNF and elsewhere within the range of the northern spotted owl. The role of hybridization as a significant force in this case remains uncertain (Kelly 2002). The more likely long-term scenario will probably involve either some amount of resource partitioning or extinction of the northern spotted owl from significant portions of its range. Optimal foraging theory and the "compression hypothesis" hold that habitat partitioning should be a more common occurrence than partitioning of other resources like diet (MacArthur and Wilson 1967, Schoener 1986). The results from the SNF indicate that partitioning at the macro-habitat level is not yet occurring. However, it is reasonable to expect some sort of niche shift to develop over time. Nonetheless, in the absence of significant niche separation, the threat of extinction must be considered due to the combination of continuing northern spotted owl population declines and a rapidly increasing population of competitors. The contribution of barred owl competition to spotted owl demographic performance needs to be assessed but preliminary evidence from Oregon and Washington showed significant declines in spotted owl site occupancy when pressured by barred owls (Kelly2002).

Why barred owls expanded into the region in the first place remains unclear. In addition to forest fragmentation, several other hypotheses have been suggested but none have been investigated. Demographic stochasticity, climate change, and shelterbelt planting in the Great Plains are all plausible explanations but are difficult to assess (Johnson 1994, Kelly 2002). Regardless of the process that triggered expansion, it is becoming increasingly clear that barred owls have now entirely overlapped and exceeded the niche breadth of the northern spotted owl throughout their range. This is complicating current spotted owl recovery efforts. It will be very difficult to develop management strategies for spotted owls while simultaneously discouraging barred owls. The barred owl will certainly play a central role in future spotted owl population dynamics. The success of spotted owl conservation will depend on how well we improve our understanding of basic barred owl life history in the northwest and the ecology of competition between the two species. We should also recognize the great value of this phenomenon to the study of competition, in general.

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