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Factors controlling distribution and demography of Northern Spotted Owls in a reserved landscape

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This is to certify that I have examined this copy of a master's thesis by

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Introduction

The Barred Owl (*Strix varia)* is a common species, whose range in the early 20th century was restricted to forested areas of North America, east of the Rocky Mountains (Bent, 1938). At that time, the species had apparently already begun a range expansion across the mixed-wood boreal forests of central Canada, with the first reliable records for both Alberta and British Columbia occurring nearly simultaneously in the early 40's (Boxall and Stepney, 1982; Grant, 1966, Houston, 1959). In 1946, Barred Owls were found nesting west of the Canadian Rockies in east-central B.C. and by the mid-70's the species was established in western Washington (Grant, 1966; Taylor and Forsman, 1976).

Today the range of the Barred Owl completely overlaps that of the congeneric Northern Spotted Owl (*Strix occidentalis caurina*), extending south into the forested regions of northern California (Dark et al., 1998). Barred Owls now outnumber Northern Spotted Owls by ratios ranging from 2.1 to 4.1:1 on Northern Spotted Owl study areas in the north Cascades of Washington and in southwest British Columbia (Dunbar, et al., 1991; Hamer, 1988; Kuntz and Christopherson, 1996). In the managed forests of the western Olympic Peninsula between the years 1991 and 1999, Barred Owl detections/station increased from 0.002 to 0.24, while Northern Spotted Owl rates declined from 0.031 to 0.009 (Wiedemeier and Horton, 2000).

When the Northern Spotted Owl was listed as threatened under the federal Endangered Species Act, the primary threat to the viability of the species was the "loss and adverse modification of suitable habitat as the result of timber harvesting…" (USDI, 1990). The primary strategy for the protection and recovery of the Northern Spotted Owl has been the designation of extensive areas of federally-owned forestland as late-successional reserves, in which most timber harvest is prohibited. Despite these efforts, the Northern Spotted Owl continues to decline across much of its range (Franklin et al., 1999).

Consistent anecdotal evidence from across the range of the Northern Spotted Owl suggests that the Barred Owl is displacing the Northern Spotted Owl from many sites. In the first effort to quantify these effects, Kelly et al. (2003) showed that occupancy rates declined significantly at Northern Spotted Owl sites following the first detection of Barred Owls within 800m of an activity center. In one reported case in California it appears a Barred Owl killed and partially ate a Northern Spotted Owl (Leskiw, 1998). The two species will hybridize, although this appears to be rare (Hamer et al., 1994; Herter and Hicks, 2000; Kelly, 2001). Because of their similarity in size, habitat and diet, a recent status review concluded that Barred Owls and Northern Spotted Owl are unlikely to coexist (Courtney, et al., 2004).

The effects of Barred Owl competition are difficult to separate from the effects of habitat changes in most studies of Northern Spotted Owls. Our study was restricted to a large reserved area where habitat changes over the last 12 years have been limited to natural disturbances and the processes of forest succession. Using data gathered incidentally while monitoring Northern Spotted Owl demographic rates, I describe here the extent which this large reserved area has been invaded by Barred Owls, and the relevance of this invasion for Northern Spotted Owl conservation efforts. The primary objective is to answer the question: Does the presence of Barred Owls affect site occupancy, movement or productivity of territorial Northern Spotted Owls?

Study Area

The study was conducted entirely within Olympic National Park (ONP), on the Olympic Peninsula in northwest Washington State. The park is 386,900 ha, of which roughly 193,500 are forested and at an appropriate elevation to be suitable Northern Spotted Owl habitat. There is a steep precipitation gradient from rainforest valleys in the southwest which receive over 300 cm annually, to rainshadow areas in the northeast which average under 80 cm/yr (Franklin and

Dyrness, 1973). As a result, east-side forests have a history of more frequent fires than west-side forests, and tend to be younger, more even-aged, and dominated by sub-climax Douglas-fir (*Pseudotsuga menziesii*) (Henderson, et al., 1989). The park's west side contains more uneven-aged, old-growth forest, dominated by shade-tolerant species such as western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*), with Douglas-fir more abundant on southern aspects. Eleven large rivers radiate from the mountainous central core of the Olympic Peninsula. As a result, elevations tend to be lowest near the park's boundary. Topography is steep, ranging from sea-level to 2428 m, and access to the park interior is limited to trails that generally follow the major river valleys. During this study there have been no major insect infestations, fires or other large-scale natural disturbances.

Methods

Site Selection, Field Methods and Study Design

My study builds on demographic monitoring at historically occupied Northern Spotted Owl territories ("sites") in Olympic National Park ($N = 52$). A site was defined by the location of all historic owl responses, generally daytime nest and roost locations, of an individual or pair of territorial Northern Spotted Owls. While some were spatially discrete clusters of detections falling less than 500m from each other, some sites represented an area over 2 km across that were traversed by a banded individual or pair. An annual site center was designated for a site each year based on a hierarchy of occupancy status; the nest site was considered the best center, followed by multiple pair sightings, or multiple locations of a single individual. Where there were not multiple locations, earlier sightings took precedence over later and female locations over male.

We began demographic monitoring to current protocols in 1992, with an initial sample of 37 sites, many of which had been monitored less formally for several years. These sites were known from trail-based surveys, random transects and the first year of random inventory plots. Between 1993 and 1996, we added 15 new sites found on random census plots to the sample. For logistical reasons, only sites that were within a day's hike of a site already being monitored were added to the sample. As of 2003, we had 8-12 year records from 52 Northern Spotted Owl territories, all of which have been occupied by a Northern Spotted Owl pair in at least one year.

Determination of site occupancy, and pair, nesting, and reproductive status of Northern Spotted Owls at each site was based on USFS Pacific Northwest Research Lab protocols (Forsman, 1995, Franklin et al., 1996). We attempted to capture and band all adults and juveniles in order to estimate survival rates using mark-recapture methods. Vocal imitations of Northern Spotted Owl calls were used to elicit responses from territorial individuals, followed by offers of live mice to determine nesting and reproductive status. Reid et al. (1999) located 94% of individuals in 3 visits using these methods. Two-person National Park Service crews visited each site a minimum of three times between mid-March and late July, or until they determined the pair, nesting and reproductive status of the Northern Spotted Owls occupying the site. Most surveys were performed during the daytime, due to the difficulties of off-trail travel at night. When Northern Spotted Owls were not found near historic locations, crews searched outward 1-2 km to locate the banded birds. A 2-km radius circle equates to the lowest pair density found in any part of ONP in a park-wide inventory (unpub. park data), and is within the range recommended by Franklin et al. (1996) based on median home range size.

When owls were found greater than 2 km from the prior activity center, the decision whether to consider this a new territory or a new site center at the former territory was based on knowledge of the area used by the banded birds at the site in the past, local topography, locations of adjacent territories and typical nearest neighbor distances for the area. In effect, there was a continuum of movement away from a former site center, which at some point we considered far enough to label that site unoccupied. Despite this subjectivity, the effect on the results of this analysis was captured in either the analysis of site movement or site occupancy.

Barred Owls respond to Northern Spotted Owl calls (Dunbar et al., 1991; Dark et al., 1998; Hamer, 1988) and we recorded all detections incidental to Northern Spotted Owl monitoring activities. Barred Owls were not marked, and sites were delineated by combining all locations within roughly 2 km of each other as a single "site" unless simultaneous locations of owls confirmed multiple territories. Barred Owl abundance (number of sites detected/year) was adjusted by the annual survey effort, as measured by the number of days monitoring teams were in the field. Barred Owls are generally more wary of humans and may be less responsive to survey efforts than Northern Spotted Owls (Courtney, et al., 2004). As a result, protocols designed to monitor Northern Spotted Owls may be less effective for Barred Owls, and annual Barred Owl occupancy and reproductive estimates should be considered minimums.

I compared the location of Northern Spotted Owl site centers in the years 1990-2003 ($N = 629$ monitored years, 52 sites), with all Barred Owl locations ($N =$ 385 detections, 60 sites) for the years 1992-2003. I categorized Northern Spotted Owl sites as Barred Owl present if Barred Owls had ever been detected within 800 m of any years' Northern Spotted Owl activity center. This distance was selected both to approximate the core area of a Northern Spotted Owl territory, as described by Bingham and Noon (1997), and the area which we most consistently searched.

I evaluated the effects of Barred Owl presence on Northern Spotted Owl pair occupancy rates, site movement, adult dispersal, elevation change and female fecundity. Where possible I used measures both within a site before and after the first Barred Owl response, and between sites with and without Barred Owl presence. Measures of change within a site should provide the strongest evidence of a cause and effect relationship. Because the predictor variable of Barred Owl presence is likely correlated with inherent differences among sites, comparisons made between sites with and without Barred Owls provide weaker, correlational evidence of Barred Owl effects.

Statistical Analysis

Occupancy- Because the number of sites with Barred Owls increased with time, I first tested for a time trend in the only sample that could function as a control in the analysis of occupancy: the Northern Spotted Owl sites which had no Barred Owl detections. Because there was no evidence for a decline in pair occupancy over time at these control sites, I proceeded with an analysis of the sites with Barred Owls present, using the non-parametric Wilcoxon signed ranks test, due to the apparent non-normal distribution of means. The unit of analysis for this paired test was the Northern Spotted Owl site before and after the first Barred Owl detection, and the response variable was the mean proportion of years that the site was occupied by a Northern Spotted Owl pair.

Movement- I analyzed the effect of Barred Owl presence on cumulative movement at Northern Spotted Owl sites that were occupied by a pair or single Northern Spotted Owl in 2003. The measure tested was the distance between the annual site center in 1992 (or the first year the site was monitored if later than 1992) and the location of the activity center in 2003. Sites were categorized by presence/absence of Barred Owls, and means were compared with *t*-tests.

I analyzed site movement and pair occupancy collectively, asking the question "in 2003, what proportion of activity centers remained both occupied by pairs and within 1 km of the activity center identified in the first year of monitoring at the site?" The 1 km cutoff was chosen *a priori* as a conservative value that would fall well inside most territory boundaries. By explicitly defining a fixed site radius, I reduced the subjectivity involved in classifying birds that exhibited large movements as either in or out of their former territory.

I quantified, but due to small sample size did not formally analyze, differences in rates of Northern Spotted Owl dispersal related to Barred Owl presence. I defined adult dispersal as movement of territorial adults between sites. Because ONP does not monitor all sites in the population, an unknown proportion of dispersing adults go undetected after dispersing, and these absolute estimates are biased low. After eliminating cases ($N = 3$) where movement was temporary (*i.e.* Northern Spotted Owls returned to the original site), and sub-adult dispersers ($N = 2$), total sample size was 16 movement histories. I categorized dispersal events based on the history of Barred Owl presence at a site: Northern Spotted Owls last detected more than two years prior to the first Barred Owl detection at a site, Northern Spotted Owls last detected less than two years before or anytime after the first Barred Owls at a site, and Northern Spotted Owls dispersing from sites with no history Barred Owl occupancy. I calculated rates of adult Northern Spotted Owl dispersal per owl year for these categories of Barred Owl presence, with the number of "owl years" equal to the sum of the number of territorial Northern Spotted Owls recorded at all the sites in the respective categories.

Changes in the elevational distribution of the Northern Spotted Owl population could arise through two processes. The first is the shift in occupied annual site centers over time, requiring that a site remain occupied to be included in the analysis. To test for this change in elevation of occupied sites, I compared the mean elevation change of sites with and without Barred Owls, using the same sample as the analysis of site movement. The mean elevation of the population could also change as a result of territories at some elevations becoming unoccupied at higher rates than others. For this, I tested for a trend (linear regression) in the mean elevation of occupied Northern Spotted Owl sites, categorized by Barred Owl presence/absence. The sample unit was the annual mean elevation ($N = 10$ years) from a fixed sample of 50 sites monitored each year from 1994-2003. These years were chosen to maximize the length of record and sample size; only 2 monitored sites were excluded from this analysis as a result of being added after 1994.

Distribution- I summarized patterns of current Barred and Northern Spotted Owl distribution by mapping recent detections of both species in the Elwha River Valley. This drainage was selected because monitored Northern Spotted Owl sites were well distributed throughout the area, and nearly 20% of Northern Spotted Owl habitat in the park is found there. Using the location data through 2003 for the 18 monitored Northern Spotted Owl sites, as well as incidental detections of both

Barred and Northern Spotted Owls, I delineated the extent of the area that now appears to be occupied exclusively by Barred Owls. I first buffered all Barred Owl locations by 800 m. Outlying observations, or sites where Northern Spotted Owls were present in 2003 despite prior Barred Owl detections, were excluded from this Barred Owl distribution. Where Barred and Northern Spotted Owls have recently been found less than 800 m apart, the boundary of the distribution was a line connecting the mid-point between current Northern Spotted Owl locations and the nearest Barred Owl detection. In the areas between monitored sites, the boundary followed the elevation of the nearest midpoint. Following the 2004 field season, I validated the Barred Owl distribution map with the 2004 Barred and Northern Spotted Owl locations.

Fecundity- Initially, I attempted to model fecundity using PROC MIXED (SAS version 8.2, SAS Institute, 1999), as described by Franklin, et al. (2004, p. 14-17) in their meta-analysis of California Spotted Owl fecundity. Mixed models allow for correct inference to the repeated measures sample unit, in this case the Spotted Owl site sampled over many years. They also do not require samples with missing data to be ignored, as would be the case with repeated measures ANOVA (Littell, et al., 1998). As there were missing values at a Northern Spotted Owl site for every year it was unoccupied, or when we failed to meet protocols for determining reproductive output, this was a primary consideration. I defined fecundity as the number of female offspring produced annually per territorial female. Assuming a 1:1 sex ratio, I divided the number of juveniles Northern Spotted Owls fledged at each site by 2 to estimate the number of female offspring, thus fecundity could take on the value of 0, 0.5 or 1. I analyzed all non-juvenile Northern Spotted Owls as a single age class to avoid discarding breeding attempts by females of unknown age. I also included all breeding attempts where we made at least one protocol visit to count juveniles, rather than the 2 visits required by the strict protocol. Monitoring protocols were designed to confirm both nesting and number of young fledged, and the fecundity values analyzed are for the annual reproductive output of a monitored female owl, whether or not she attempted to nest.

Modeling of the covariance structure in PROC MIXED suggested that there was little correlation within sites or years. Fitting a general linear model to the fecundity data also showed virtually no overdispersion resulting from within year or within site correlations. Because of this, I used a paired t-test to estimate Barred Owl effects on Northern Spotted Owl fecundity. This analysis treated multiple reproductive attempts at a site as independent, while maintaining the effect of year as the pairing factor, thus treating year as a random effect. In this analysis, the mean fecundity at sites with Barred Owls was compared with the mean for that year at sites without Barred Owls. Means of fecundity estimates were calculated on the mean of these unweighted averages, with $N = 12$ years. I also compared within site changes in fecundity at sites having fecundity records both before and after the first Barred Owls were detected. As with the occupancy analysis, I used a linear regression to test for changes over time in the "control" sample of 16 sites without Barred Owls in any year.

Except where noted, statistical tests were performed in SPSS, version 12.0 (SPSS 2004). All groups were examined for normality and homogeneity of variance before applying parametric statistics. All tests were performed two-tailed. I reported means (SD), and used a statistical significance level of 0.05.

RESULTS

Barred Owl abundance and distribution

Barred Owls were first reported in ONP in 1985, when they were found at four sites (Sharpe, 1989). By the beginning of the current study in 1992, ONP crews had located 15 Barred Owl sites. From two to six new Barred Owl locations were detected each year from 1992 to 2003, when the total number of known territories reached 60. The number of occupied Barred Owl sites detected /team-day in the field increased over this period at a rate of 15% per year (Figure 1.1). By 2003, the ratio of occupied Barred Owl sites to Northern Spotted Owl sites was 0.8: 1. Given that survey efforts focused on recent Northern Spotted Owl locations and therefore avoided areas heavily used by Barred Owls, it is likely that the number of

Barred Owls had equaled or exceeded the number of Northern Spotted Owls in ONP by this time.

On the Olympic Peninsula, Barred Owls were initially found in lowland floodplain forests near the park's western boundary. The first sightings on the park's drier east side were in 1990, also near lakes and riparian areas. Through the 1990's, Barred Owls were found farther up river valleys each year and are now established in all major drainages in which we survey. From 1985 to the present, Barred Owls have been found over an increasing range of elevations (Figure 1.2). Similarly, the range of elevations of Barred Owl sites where reproduction has been recorded has increased over time. Although Barred Owls now occupy all of the forest types used by Northern Spotted Owls, most reproductive pairs were found in low elevation areas with a component of riparian forest or wetland. Only two of 19 successful Barred Owl nests on the east side were above 600 m and only one of 12 west-side nests was above 200 m.

Both Spotted and Barred Owls were found at significantly lower elevations on the park's (wetter) west side than on the east. The mean elevation of Barred Owl locations was significantly lower than the mean for Northern Spotted Owls in 2003, both overall and by geographic locale (Table 1.1).

In 1992, Barred Owls had been found within 800 meters of four of the 35 Northern Spotted Owl sites being monitored. By 2003, Barred Owls had been found within 800 m of at least one annual activity center at 36 of the 52 monitored Northern Spotted Owl sites. After the first year they were detected at a Northern Spotted Owl site, Barred Owls were found in 36% of subsequent years, when calculated over all sites with three or more years since Barred Owls were detected (*i.e.* sites with Barred Owls prior to 2002, $N = 32$). Barred Owls were detected in over 75% of subsequent years at three sites, and less than 25% of subsequent years at 13 sites. The latter group included 4 sites where Barred Owls were never relocated within 800m after the first record.

Barred Owl effects on Northern Spotted Owls

Occupancy- A linear regression of pair occupancy versus time at the control sites (Northern Spotted Owl sites without Barred Owls) showed a weak, non-significant increase in pair occupancy over the period of study (beta = 0.008, 95%CI = -0.015, 0.030). At sites with Barred Owls, the rate of Northern Spotted Owl pair occupancy declined following the first Barred Owl detection at a site, from a mean of 60.6% to 41.6% (Wilcoxon sign test, $Z = 2.57$, df = 30, $p = 0.01$). Pair occupancy declined at 23 sites, increased at 6, and remained the same at 2. In addition to these within-site declines, there was a consistent difference between sites with and without prior Barred Owls. In 11 of 12 years, occupancy rates were higher at sites without prior Barred Owls, the exception being the first year of the study when Barred Owls were present at only 5 sites. In 2003, Northern Spotted Owl pairs were present at 69% of sites where Barred Owls were absent, compared to 33% of sites where Barred Owls had been present (X^2 with continuity correction = 4.29, df = 1, $p = 0.04$). The mean pair occupancy rate at the 16 control sites over all years was similar to that at the remaining sites prior to the first Barred Owl detection (64% and 61% respectively). Nine of the 10 Northern Spotted Owl sites not occupied by pairs in any of the last five years were those with Barred Owl detections.

Movement- Between the first year of monitoring and 2003, activity centers at Northern Spotted Owl sites that remained occupied in the presence of Barred Owls shifted nearly twice as far as at sites without Barred Owls (Table 1.2). This trend was consistent on both the east and west sides of the park, but not significant for the small west-side sample despite the larger difference in movement. There was no evidence that the Northern Spotted Owl sites with Barred Owls had a greater tendency to move prior to the first Barred Owl detection, relative to Northern Spotted Owl sites without Barred Owls (Appendix 1).

Northern Spotted Owls either shifted their activity centers within a territory, or abandoned the territory entirely following the first Barred Owl detection in nearly all observed cases. When pair occupancy was limited to Northern Spotted Owls remaining within 1 km of the initial location at a site, 63% of Northern Spotted Owl sites with no Barred Owls were occupied in 2003, compared to 14% of sites with prior Barred Owl detections (X^2 with continuity correction = 10.494, df = 1, p = 0.001). There was little evidence for co-existence, even at the five sites where Northern Spotted Owls remained within 1 km of their initial location following a Barred Owl detection. Only one of these sites remained occupied by Northern Spotted Owls following several years of Barred Owl occupancy. At this site, Barred Owls were found less than 400 m from the Northern Spotted Owl activity center five times between 1995 and 1998, including some visits where both species were detected. At two sites, Northern Spotted Owls temporarily moved from the activity center for 1-3 years following the first Barred Owl detection, and no Barred Owls have been detected since their return. Another site had only a single Barred Owl detection at an active Northern Spotted Owl nest, and the resident Northern Spotted Owls remained and reproduced successfully. A fifth site historically alternated between two activity centers, one of which has been occupied by Barred Owls. There was little net movement at this site because Northern Spotted Owls now occupy the initial activity center, where there have been no Barred Owl detections.

Among the 16 identified cases of adult dispersal by territorial Northern Spotted Owls, 15 were from sites with Barred Owls. Eleven of these Northern Spotted Owls were last located at the original site either within the two years prior to, or sometime after, the first Barred Owl. Four Northern Spotted Owls dispersed more than 2 years before the first Barred Owls were found at a site. Only one territorial Northern Spotted Owl dispersed from a site without Barred Owls. The dispersal rate at sites less than 2 years before or anytime after the first Barred Owl detection (N = 336 owl years) was 3.3% a year, and Northern Spotted Owls dispersed at a rate of 2.1% per year from sites more than 2 years before the first Barred Owl detection (N = 190 owl years). At sites where Barred Owls were absent (N = 258 owl years), adult Northern Spotted Owls dispersed at a rate of 0.4% a year.

Both measures of Northern Spotted Owl elevation change showed a correlation between the presence of Barred Owls and increasing Northern Spotted Owl site elevations. When Northern Spotted Owl sites remained occupied (pair or single) in the presence of Barred Owls, activity centers increased in elevation relative to sites with no Barred Owls (Table 1.3). The differences between the means were greatest for the east-side sites; the small sample of west-side sites showed no effect from Barred Owls. Tests for linear trends in the sample mean elevation had similar results. There was no evidence for a change in mean elevation at Northern Spotted Owl sites where Barred Owls were absent (Table 1.4). In the presence of Barred Owls, the mean elevation of the monitored Northern Spotted Owl sites increased over time. With a 95% level of confidence, the mean increase over the 10-year period at all Northern Spotted Owl sites with Barred Owls ranged from 51 to 193 m (167-633').

Changes in distribution: Elwha case study- I mapped the area now occupied exclusively by Barred Owls in the Elwha Valley using 133 Barred Owl detections from 1992 to 2003, and the locations where Northern Spotted Owls remained in 2003 (Figure 1.3). This zone extends from the river to around 610m (2000') in most of the lower valley, and around 730m (2400') in the upper valley. In the first five years of monitoring, an average of 33% of the occupied Northern Spotted Owl sites in the valley were located within this area, but this percentage declined steadily beginning in 1993, reaching zero in 2003. The range of Barred Owls in the Elwha Valley now overlaps 25,000 acres of the 98,000 acres of suitable Northern Spotted Owl habitat. At many Northern Spotted Owl sites, only a thin strip of habitat remains above the areas now occupied by Barred Owls, and several sites with little habitat available above this zone have not been occupied by Northern Spotted Owls for 10 years. The area without Barred Owls in the middle of the river corridor is a steep canyon with little riparian vegetation.

Owl locations from the 2004 field season were used to validate the accuracy of this map. Twelve of 18 monitored Northern Spotted Owl sites in the Elwha

Valley were occupied in 2004, and a single Northern Spotted Owl in the upper valley fell inside the polygon by 22 meters, for a classification accuracy of 92%. There were 30 Barred Owl detections recorded in the Elwha in 2004. Of these, 24 fell inside the Barred Owl polygon and 6 were outside, for a classification accuracy of 80%. New Barred Owl detections, all in areas which were well surveyed over the last 12 years, expanded the area where this species was found. There was evidence of immediate exclusion of Northern Spotted Owls at the four Northern Spotted Owl sites near these new Barred Owl locations; two had no Northern Spotted Owl responses and two moved upslope an average of 275 meters (900') in elevation, successfully fledging young at new nest sites.

Fecundity- When paired by years, there was little difference in Northern Spotted Owl fecundity between sites with and without Barred Owls (respective means (SE), 0.270 (0.079) and 0.289 (0.087), $t_{11(2)} = 0.549$, $p = 0.594$. Within sites, changes in fecundity were evaluated at 21 Northern Spotted Owl sites with at least one fecundity record before and after the first Barred Owl detection near that site. The absolute differences in means were greater than the between site comparisons, but were not statistically significant (means (SE) before and after Barred respectively, 0.294 (0.059) and 0.418 (0.070), $t_{20(2)} = 1.275$, $p = 0.217$). In addition, the regression of fecundity at sites prior to Barred Owls indicated a non-significant, but downward trend in time at these sites (slope coefficient for year = -0.007, $p =$ 0.766). If the point estimate of this time trend is accurate, it would account for some of the decrease found after Barred Owls were located at a site.

DISCUSSION

In the large, forested reserve of Olympic National Park, Northern Spotted Owls appear to be in the process of being displaced by Barred Owls. Northern Spotted Owl sites are less likely to be occupied, more likely to move, and more likely to increase in elevation after Barred Owls are detected nearby. The net result of competition between these species in ONP appears to be a change in the distribution of Northern Spotted Owls, as Barred Owls exclude many Northern Spotted Owls from all or part of their former territories. This loss may represent over 25% of the otherwise suitable old-forest habitat in one of the largest river drainages in the park, and there is evidence that Barred Owls continue to increase in numbers. The combined analysis of occupancy and movement provides the most compelling evidence that Northern Spotted Owls move to avoid Barred Owls in most instances, either abandoning a territory altogether, or relocating away from the Barred Owls. The higher rates of Northern Spotted Owl dispersal from sites with Barred Owls also support this hypothesis. The design of this study was opportunistic, not strictly experimental. While the results are correlational, they are replicated at 52 Northern Spotted Owl sites, and include time series data from up to 12 years of monitoring, including four years after the working hypotheses were first proposed, and as such are only partially retrospective.

My results provide one potential mechanism for the steep declines in Northern Spotted Owl populations observed in Washington State (Anthony, et al., 2004). While the Northern Spotted Owl has declined range-wide, these declines are most rapid in Washington State, where Barred Owls have been both most abundant and present for the longest time. Anthony et al. (2004) also included an exploratory Barred Owl covariate, measured at the study area level, which appeared in the best survival model for the Olympic Peninsula study area. While this covariate was much more correlational, showing overall survival rates of Northern Spotted Owls inversely correlated with increasing Barred Owl populations in the Olympics, this study shows a stronger territory specific association of Barred Owls with declining occupancy. The net loss of available Northern Spotted Owl habitat due to Barred Owls should result in either lower survival or productivity, as density dependent factors bring the population back to equilibrium in a smaller area. Fecundity appears to be stable, and some evidence suggests that the effects of displacement may be showing up in lowered adult female survival.

The mechanism of displacement could be either direct or indirect. The trends in Northern Spotted Owl movement and occupancy following barred owl detections, with fecundity remaining stable, are consistent with a hypothesis of interference competition by aggressive displacement of Northern Spotted Owls by Barred Owls. There is much anecdotal evidence to support the fact that Barred Owls are dominant over Northern Spotted Owls in interactions (Courtney, et al., 2004, p. 7-25). In fact, with few exceptions, there is little to suggest that Barred and Northern Spotted Owls ever coexist at a given point for any length of time in ONP. It appears that Northern Spotted Owls are excluded quickly from sites, with little time for competition for food resources. While both species are occasionally detected near each other in the initial period of contact at a site, only a single Northern Spotted Owl site where Barred Owls were detected more than once has not ultimately been displaced.

I cannot completely discount the possibility that Northern Spotted Owl occupancy rates decline at a site after Barred Owls move in only because the Northern Spotted Owls become secretive and difficult to detect. However, in many cases the former territory holders were relocated significant distances from their previous activity center following Barred Owl occupancy of the site. In other cases the Northern Spotted Owls were simply never seen again. A recent meta-analysis of Northern Spotted Owl data included annual estimates of recapture probabilities for all monitored Northern Spotted Owls on the Olympic Peninsula, including those on Olympic National Forest and ONP (Anthony, et al., 2004, in press, appendix G). These values ranged from 0.67-0.84 in the years 1992-2003, except for an outlying value of 0.3 in 1999 when record snowpack resulted in few owl detections in the usual summer core areas. These rates would be difficult to maintain if the detection rates of Northern Spotted Owls at the sites with Barred Owls were approaching zero. We have no evidence for cryptic behavior, in the form of re-sightings of missing individuals or pairs in the same location after several years of non-detection. When missing individuals are relocated, it has generally been at some distance from their last sighting. Additionally, there are many ways to detect Northern Spotted Owls that do not rely on vocalizations. Of the 49 Northern Spotted Owl detections recorded in the first 2 months of the 2004 field season, 27%

were first detected visually, primarily as a result of owls flying in to investigate owl surveyors, or owl surveyors investigating the agitated calls of songbirds mobbing an owl. Pellets, whitewash, and juvenile vocalizations also indicate nest and roost sites by means other than adult vocal responses, although they do not immediately differentiate between Barred and Northern Spotted Owls. Finally, shed feathers are often identifiable to species and provide supporting evidence of the *Strix* species present at a site.

The Barred Owl confounds efforts to protect the Northern Spotted Owl in large reserves. It also provides a case study of the failure of the umbrella species concept (Caro and O'doherty, 1999) when the fate of the umbrella species is driven by factors in addition to habitat loss. Due to the politicized nature of the debate over anything having to do with the Northern Spotted Owl, there will be those who will seize on this issue as evidence that habitat loss is no longer a threat to the Northern Spotted Owl. Others will demand larger reserves for the species. In fact, what may be needed is a shift in focus toward protecting sites that may function as refugia, and these sites may not look like the classic old-growth often associated with Northern Spotted Owl habitat. The species appears to be increasingly restricted to steep slopes, headwaters, and higher elevations, all typically less productive forest types. In managed landscapes this may be fortuitous, as these are often the sites most likely to remain unharvested. In the Olympics, low-elevation riparian forests may no longer be suitable Northern Spotted Owl habitat, regardless of stand age or structure. The Northwest Forest Plan placed 2.23 million acres in riparian reserves, 9% of the total acreage covered by the plan. (USDA and USDI, 1993) While this acreage was not included in calculations of protected Northern Spotted Owl habitat, this was only due to the lack of information on Northern Spotted Owl occurrence in these corridors.

Both the pattern of invasion of the Olympic Mountains and the location of the most productive nests suggest that the highest quality Barred Owl habitat is low elevation, relatively level forest, often with a component of deciduous trees (alder) and wetlands. However, it also appears that single Barred Owls can successfully colonize nearly any forest type and displace Northern Spotted Owls, even where there is no evidence that the Barred Owls are successfully pairing or reproducing.

In the Cascade Mountains, Barred Owls nest at both lower and higher elevations than Northern Spotted Owls (Herter and Hicks, 2000). In the Olympic Mountains, Barred Owls have consistently occurred at lower elevations than Northern Spotted Owls. Where both species occur in the same general area, Northern Spotted Owls have in all cases been the higher elevation species, generally separated from Barred Owls by >250 m of elevation. This apparently non-random habitat partitioning makes elevation a useful surrogate predictor of the likelihood that Barred Owls will occupy a site, or inversely, of where Northern Spotted Owls will persist. While Barred Owl populations continue to expand, it is impossible to know if there is enough separation in the ecological niches of the two species to permit them to co-exist. It does appear that as Barred Owl density has increased, the niche separation between Barred and Northern Spotted Owls has narrowed.

The presence or absence of Barred Owls will also confound efforts to model Northern Spotted Owl distribution based on habitat condition and trend. The monitoring component of the Northwest Forest Plan calls for a shift from demographic monitoring to habitat-based predictive models to measure the success of the plan in stabilizing populations of the northern Northern Spotted Owl (Lint, et al., 1999). Clearly, including Barred Owl occurrence as a covariate in these models, as recommended by Kelly, et al. (2003), will be necessary in regions where this species is abundant. However information on Barred Owl presence is incomplete, even where Northern Spotted Owl survey effort has been consistent, and there is little published information that would allow Barred Owl occurrence to be predicted by habitat models. As a result, Barred Owl competition will probably extend the time needed to predict Northern Spotted Owl vital rates and population trends by any means other than on-site demographic monitoring.

The results of this analysis, along with those of Kelly et al. (2003), Pearson and Livezy (2003), and the consistent observations of owl researchers across the range of the Northern Spotted Owl provide strong evidence for displacement of

Northern Spotted Owls by Barred Owls. All of these studies were opportunistic and each approached the question of Barred Owl effects with slightly different questions and methodologies. However, the consistency of the results provides multiple lines of evidence in support of the theory that Barred Owls displace Northern Spotted Owls. The different patterns of Northern Spotted Owl response and Barred Owl distribution within ONP echo the results of Herter and Hicks (2000) and Pearson and Livezy (2003) in the Washington Cascades. Both groups described similar Barred Owl habitat preferences, with the species most abundant in moist, relatively level, low elevation sites. Herter and Hicks (2000) observed that habitat separation between Barred and Northern Spotted Owls was greatest in dry areas. The same pattern was apparent in the Olympics, where there was evidence that stable territories of both species segregated at a finer scale by elevation or landscape position on the dry east side. There was less evidence for this on the west side, where Northern Spotted Owls coexisting with Barred Owls moved greater distances, but tended to remain at the same elevation. It is too soon to tell if the results of these studies, which took place in Washington and Oregon, might apply to California as Barred Owls colonize suitable habitat there. Initial indications are that in California, Barred Owls are becoming most abundant in the redwood zone, the moist, productive, low elevation analogue to our Sitka Spruce forest type (Redwood NP, unp. data).

Two research topics would provide information to guide Northern Spotted Owl conservation efforts in the face of Barred Owl competition. There is a critical need to identify the sites least likely to be displaced by Barred Owls and the factors that might predict Barred Owl occupancy. There is also a need to investigate the extent which Northern Spotted Owls might continue to use areas also used by Barred Owls. In ONP, it appears that Northern Spotted Owls are not using these areas for nest or daytime roost sites, but it is unknown whether these regions might be used for night-time foraging, dispersal, or even daytime roost sites by non-territorial adults. A carefully designed, replicated, removal experiment, advocated by Courtney et al. (2004), would address both of these issues. If removal proves impossible for political or biological reasons, it would be valuable to radio-track both species at locations where their territories are adjacent in order to investigate the degree of overlap, and finer scale habitat use.

Northern Spotted Owl distribution has changed dramatically in the 12 years of monitoring at Olympic National Park, one of the largest and least altered reserves within the species' range. However, there still exists a considerable acreage of Northern Spotted Owl habitat unaffected by Barred Owls. With Barred Owl populations apparently still increasing in numbers and range, any prediction of the ultimate outcome here or elsewhere would be speculative. Until the interactions between these species are better understood, it may be necessary to increase protection of Northern Spotted Owl sites that remain occupied, even those in marginal habitat, in order to keep options open for future management. However, in the long term, society may have more difficult decisions to make regarding the Northern Spotted Owl.

Table 1.1. Mean elevation in meters of occupied (pair or single) Barred and Northern Spotted Owl sites, 2003.

	Spotted Owls		*Barred Owls*	
	n	*mean (SD)*	*n*	*mean (SD)*
East side	28	830 (174.5)	20	559 (218.2)
West side	7	481 (200.0)	8	122 (71.8)
All sites	35	760 (226.7)	28	434 (274.2)

t- tests of all Spotted and Barred Owl means differ with p<.001

Table 1.2. Mean distance in meters (SD) of 2003 activity centers from 1992 locations (or first year monitored if later) for all sites occupied by a pair or single Northern Spotted Owl in 2003. Comparisons are between Spotted Owl sites where Barred Owls have been present and those where they were absent.

	n	*Barred Owl absent*	*n*	*Barred Owl present*	*t*	*p*
East side	11	637 (498.5)	17	1264 (782.6)	2.357	0.026
West side	4	536 (187.6)	3	1569 (1340.7)	1.572	0.177
All sites	15	610 (432.7)	20	1310 (847.1)	3.181	0.006

Table 1.3. Mean elevation change in meters (SD) of Northern Spotted Owl activity centers occupied by a pair or single in 2003 ($n = 35$) from 1992 locations (or first year monitored if later). Comparisons are between Spotted Owl sites where Barred Owls were present and those where they were absent.

	Barred Owl absent		*Barred Owl present*			
	n	*mean (SD)*	*n*	*mean (SD)*	*t*	*p*
East side	11	-76 (171.2)	17	118 (188.1)	2.75	0.01
West side	4	-75 (118.4)	3	-73 (139.7)	0.02	0.96
All sites	15	-76 (154.8)	20	89 (191.7)	2.73	0.01

Table 1.4. Regression results for Northern Spotted Owl sample mean elevations. Beta values are mean annual elevation change in meters of Northern Spotted Owl locations at a fixed sample of 50 sites. Number of sites is given for each category, but annual means were calculated only on the Northern Spotted Owl sites occupied in that year, and sample size for regressions and standard errors was $N = 10$ years.

	Barred Owl absent				*Barred Owl present*			
			95% CI				*95% CI*	
	# sites	*beta*	*lower*	*upper*	*# sites*	*beta*	*lower*	*upper*
East side	10	-2.4	-15.9	11.1	29	15.6	7.5	23.7
West side	5	-0.9	-12.1	10.4	6	-1.9	-15.9	12.1
All sites	15	3.0	-8.6	14.7	35	12.2	5.1	19.3

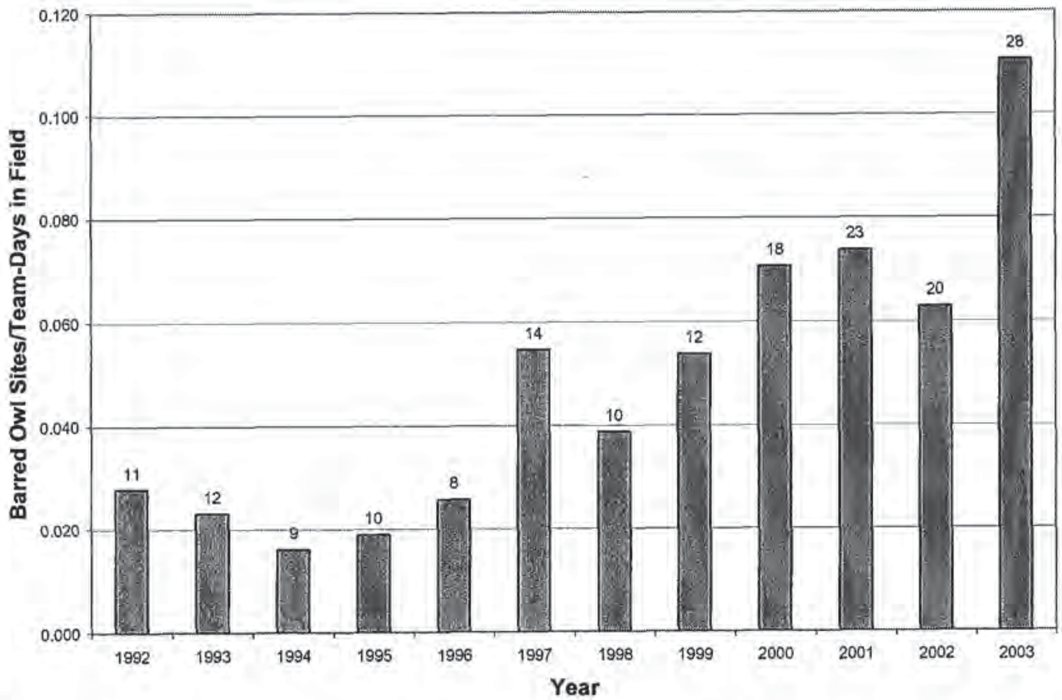

Figure 1.1: Number of Barred Owl sites detected annually, expressed per field days worked by Spotted Owl survey teams. Team-days in field ranged from 396-560 prior to 1996, and 223-318 from 1996-2003. Each bar is also labeled by the uncorrected count of Barred Owl sites for that year.

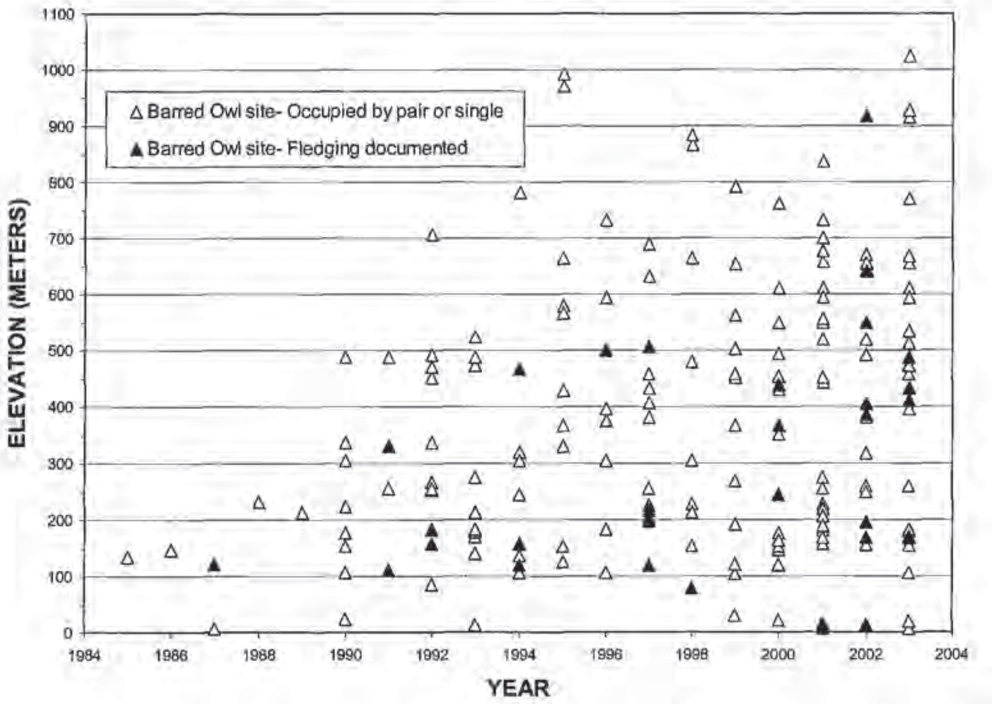

Figure 1.2. Distribution of Barred Owl sites by elevation and reproductive status for years 1984-2003. Sites were not formally monitored for reproductive status, and many additional occupied sites likely produced young. One outlying observation above 1400 m in 1993 is not shown.

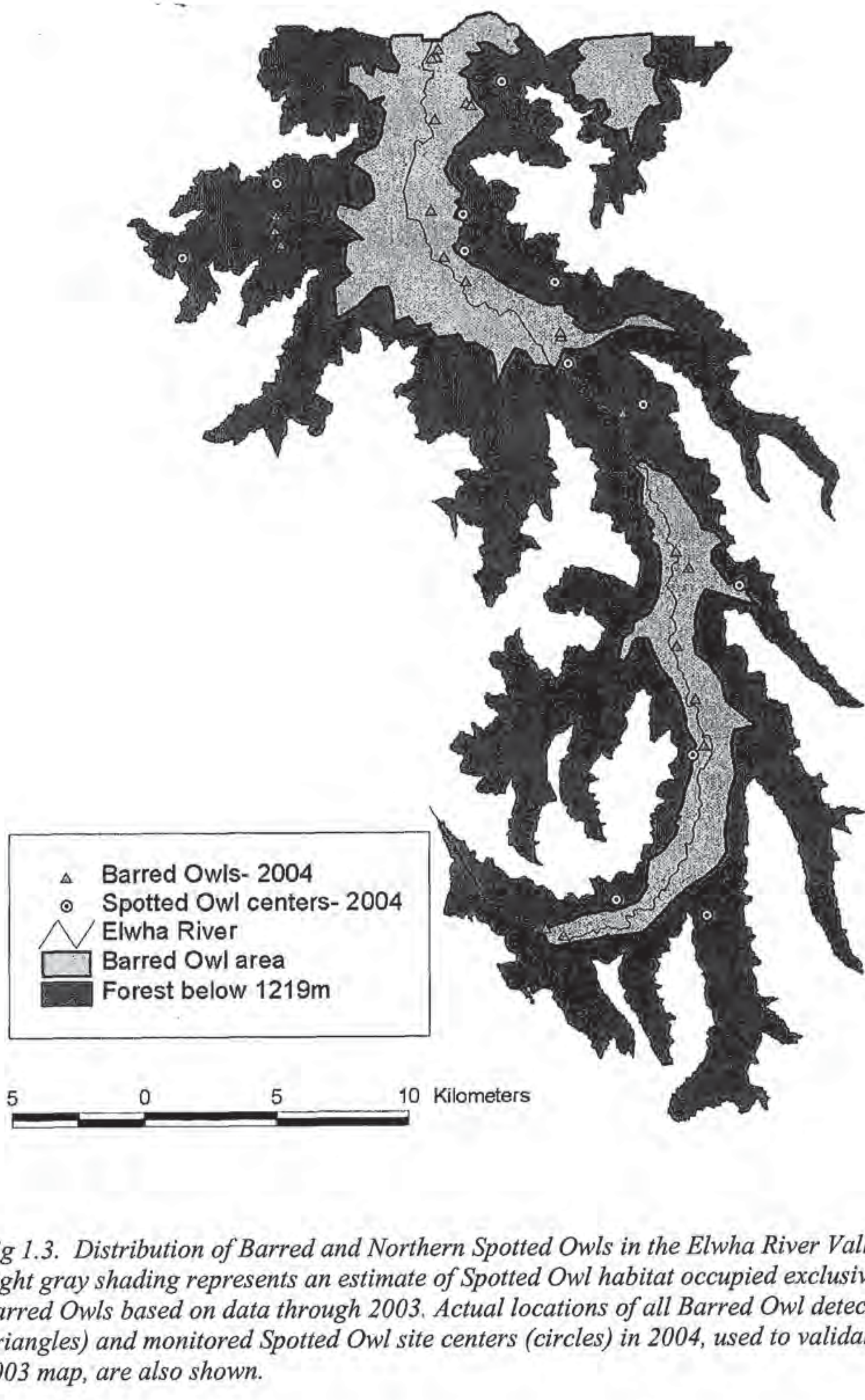

Fig 1.3. Distribution of Barred and Northern Spotted Owls in the Elwha River Valley. Light gray shading represents an estimate of Spotted Owl habitat occupied exclusively by Barred Owls based on data through 2003. Actual locations of all Barred Owl detections (triangles) and monitored Spotted Owl site centers (circles) in 2004, used to validate the 2003 map, are also shown.

Chapter 2: What habitat features are correlated with Barred Owl occurrence at Northern Spotted Owl centers of activity?

Introduction

The Barred Owl (*Strix varia*) is a recent addition to the avifauna of the Pacific Northwest, only reaching British Columbia in the mid-1940's (Boxall and Stepney, 1982; Grant, 1966, Houston, 1959; Bent, 1938). Whether this range expansion was facilitated by anthropogenic changes in the landscape, (e.g. changes in forest structure resulting from fire exclusion as hypothesized by Wright and Hayward (1998)), climate change (Johnson, 1994), or other factors, is not known, but the impacts of this invasion on the threatened, and congeneric Northern Spotted Owl (*Strix occidentalis caurina*) are becoming increasingly obvious. Once west of the Rocky Mountains, Barred Owls colonized the entire range of the Northern Spotted Owl within 50 years, reaching western Washington in the mid-1970's (Grant, 1966; Taylor and Forsman, 1976) and the southern extent of the Northern Spotted Owl's range by the late-1990's (Dark et al., 1998).

When Barred Owls contact Northern Spotted Owls, they often displace them. (Kelly et al. 2003; Pearson and Livezy, 2003; Chapter 1). Although the mechanism of displacement is not known, similarity in habitat use is often at the root of the explanation (Kelly et al., 2003, Pearson and Livezy, 2003, Herter and Hicks, 2000). Although there is clearly overlap in habitat used by Barred and Northern Spotted Owls in the Pacific Northwest, available evidence suggests that are also some differences. We have found that Northern Spotted Owl sites in the Olympics are significantly higher in elevation than Barred Owl sites (Chapter 1). In the Southern Cascades of Washington, Pearson and Livezy (2003) documented significant differences in the elevation, slope (steeper at Northern Spotted Owl sites) and mean forest age (older at Northern Spotted Owl sites) between the two species. In the central Cascades of Washington, Northern Spotted Owl sites contained significantly more mature (100+ year-old) forest within 800m than did Barred Owl sites (Herter and Hicks, 2000). Buchanan et al. (2004) found that Northern Spotted Owl nests occurred on steeper slopes and farther from water than Barred Owl nests. Anecdotally, all these authors, as well as Dunbar, et al. (1991), noted that Barred Owls were often found along riparian corridors and valley bottoms.

The goal of this exploratory study was to identify attributes of Northern Spotted Owl habitat in Olympic National Park (ONP) least likely to be occupied by Barred Owls. I first determined whether factors known or suspected to be important predictors of Barred Owl occupancy predicted their occurrence in ONP. I then explored a variety of variables to suggest further testable hypotheses about Barred Owl habitat. This information should allow a better understanding of where Barred and Northern Spotted Owl conflicts are most likely, as well as which locations Northern Spotted Owls are most likely to continue to occupy in ONP and elsewhere. Managers could use this information to reduce interspecific interactions through habitat manipulation or focus habitat protection efforts on the sites least likely to be used by Barred Owls.

Methods

Study Area

The study was conducted entirely within Olympic National Park, on the Olympic Peninsula in northwest Washington State. The park consists of 386,900 hectares, of which roughly 193,500 hectares are forested and at an appropriate elevation to be suitable Northern Spotted Owl habitat. Details on the vegetation and topography are in Chapter 1, and Henderson et al. (1989). During the period of this study there have been no major insect infestations, fires, or other large-scale stand replacing events.

Northern Spotted Owls have been studied intensively throughout ONP since 1992 (Anthony, et al., 2004). The park-wide estimate of Northern Spotted Owl abundance was 229 pairs (90% CI+- 71) in 1995 (Seaman et al., 1996). Since 1992, ONP has monitored occupancy, fecundity and survival for 8-12 years at 52 Northern

Spotted Owl territories. All monitored territories have been occupied by a Northern Spotted Owl pair in at least one year.

Site selection

Sampled Northern Spotted Owl sites were drawn from those in ONP's demographic monitoring program. Some were initially located on trail-based surveys in the late 80's and early 90's, others from randomly located census plots surveyed 1992-1995. All have been monitored annually to assess site occupancy, and pair, nesting, and reproductive status using USFS Pacific Northwest Research Lab protocols (Franklin, et al., 1996). A single location ("annual site center") was designated for a site each year, based on a hierarchy of occupancy status. The nest site was considered the best center, followed by multiple pair sightings, or multiple locations of a single individual. Where there were not multiple locations, earlier sightings took precedence over later, and female locations over male. At any given time, over 80-90% of adults on monitored territories were color banded, which allowed adjacent activity centers to be accurately assigned to sites.

Barred Owls were located incidentally during ONP's Northern Spotted Owl monitoring efforts when they responded to surveyor's Northern Spotted Owl calls (Dunbar et al., 1991; Dark et al., 1998; Hamer, 1988). Park crews also located Barred Owls when they gave unsolicited calls or were seen flying silently. Barred Owls were not marked, and sites were delineated by combining all locations within roughly 2 km of each other as a single territory, unless simultaneous locations of owls confirmed multiple territories. As of 2003, there were 64 known Barred Owl activity centers in ONP. I sampled habitat characteristics at all Barred Owl sites (N = 19) that had either 3 years of occupancy at an activity center or any evidence of reproduction. Locations were based on daytime detections (N = 168) at these sites between 1992 and 2001.

I did not sample sites that fell into this category and were located in the Queets valley (one site) or ONP's coastal strip (two sites), both areas where we have not monitored Northern Spotted Owls. I also did not sample one site that fell in a developed area with extensive non-forest.

I sampled habitat characteristics at 46 Northern Spotted Owl sites that had an annual activity center occupied for multiple years. Locations were based on summary annual activity centers at these sites ($N = 279$) between the years 1992 and 2000. Six of the 52 Northern Spotted Owl sites in ONP's monitoring program were not sampled for the following reasons: no single location occupied in multiple years (four sites), incomplete monitoring record (one site), and inaccessible (one site on cliff face).

The study population of both species, while not strictly random, was drawn from a larger known population based on objective criteria, and should be representative of habitats used within ONP. Because sampling focused on Northern Spotted Owl sites, Barred Owl locations are biased towards those most similar to sites used by Northern Spotted Owls. Barred Owls are known to use a wider range of habitat types, and broadening the study population to sites in more human-modified landscapes would result in more divergent habitat associations between the two species.

Habitat measurement

I sampled stand-level habitat characteristics on a 9-ha (after Irwin et al. 2000) grid at both Barred and Northern Spotted Owl activity centers (2.1). The scale of sampling reflected a trade-off between sampling a large enough area to encompass multiple years' activity centers and a small enough area to prevent sampling across such a wide range of stand conditions that the resulting average values would have had little meaning. At each site a 300x300m-plot was placed to encompass the greatest number of annual site centers, and then adjusted to cover the greatest number of actual daytime owl locations in those years

Nine points were located at 150 m spacing within the 9-ha grid. Information on plant association and stand age was recorded at all nine points of the grid. Plant associations measure potential vegetation developed for the area, following

Henderson et al. (1989), and were used to estimate topographic moisture ratings (Table 2.1. Disturbance history was estimated by coring 3-16 trees at each site to establish the age of the youngest class of trees originating from stand-replacing disturbance, defined as any event affecting over 10% of the plot area.

I sampled stand composition and structure within 10- and 20- m radius nested plots centered on four points: the center point of the grid and three of the four cardinal directions. If any of the four cardinal points were more than 100 m from an actual owl location, the point farthest from an owl location was dropped, otherwise the three points were randomly selected. Within the 10-m radius plot, slope and aspect were measured from the highest to the lowest point. Cover was estimated visually in seven potentially overlapping class groupings: fern, deciduous shrub, evergreen shrub, grass, forb, conifer seedling and bare ground/duff/moss. I recorded the species and diameter of live and dead trees greater than 10 cm diameter at breast height (dbh), as well as the presence of large diameter branches and top condition of trees greater than 80 cm. I assigned snags a decay class of 1 (recent dead) to 3 (soft and highly decayed) (modified from 5 classes in Cline, et al., 1980) and visually estimated snag height. I tallied saplings by species and estimated the volume and decay class (determined as above) of coarse woody debris within a 4 X 20-m strip plot.

Large, infrequently encountered habitat elements were also tallied in the outer 10-20 m radius ring of the nested plots. This included trees greater than 80 cm dbh, and snags greater than 60 cm dbh.

I calculated landscape scale habitat attributes using Arcview, version 3.2 (Environmental Systems Research Institute, Redlands, CA) (Table 2.1).

Statistical Analysis

I compared habitat characteristics between two groupings of sites: sites centered on Barred Owl activity centers versus sites centered on Northern Spotted Owl activity centers, and Northern Spotted Owl activity centers with and without a history of Barred Owl detections. In the comparison of activity centers used by the two species, the sample units were the 65 plots, and the response variable was either 0 (occupancy by Northern Spotted Owl, $N = 46$) or 1 (occupancy by Barred Owl, $N = 19$). In this analysis, the sampling universe was all forested habitat in ONP that was occupied by a *Strix* owl species. In the second grouping, I divided the 45 Northern Spotted Owl centered sites into those with (N =18) and without (N = 28) Barred Owl responses, keeping the occurrence of Barred Owls as the event being modeled. Northern Spotted Owl plots were classified as having Barred Owl presence if Barred Owls were ever detected within a 500m radius of the center of the vegetation plots. This radius incorporated the vegetation plot and a surrounding buffer of approximately 250 meters. Although Barred Owls have been shown to influence Northern Spotted Owls at greater distances than this, I was interested in correlating Barred Owl presence with attributes measured in the vegetation plots. In this analysis, the sampling universe was limited to forest that was known to be suitable Northern Spotted Owl habitat, and I expected that due to the limited scale of sampling there would be fewer differences between the groups. For both analyses, all independent variables were either means derived from forest sampling plots at the site, or map-calculated values related to distance from the plot center.

Within the two groups described above, I evaluated logistic regression models (due to the binary nature of the outcome variable) using SAS PROC LOGISTIC (SAS Institute,Cary, NC). The goal of this analysis was to select the best fitting model as measured by the small sample variant of Akaike's Information Criteria, AIC_c (Burnham and Anderson, 2000, p. 70). Models with ΔAIC_c values less than roughly two are considered to have a substantial level of support (Burnham and Anderson, 2000, p. 70). The goal of this study was not to find one best model, but to identify the factors most important in predicting the presence of Barred Owls within suitable Northern Spotted Owl habitat, as well as their direction and magnitude. I used the best ranked model containing a variable to obtain an estimate of the coefficient and standard error of each variable of interest. Coefficients in logistic regression are most interpretable as odds ratios, and I report point estimates and 95% likelihood ratio confidence intervals of the odds ratios for selected covariates.

I approached the issue of which variables to include in the model set in two ways. Prior to examining the data for within-group differences, I selected a small subset of variables (Table 2.2) based on biological hypotheses, anecdotal observations in similar landscapes, and literature review (Burnham and Anderson, 2000). Little is known about the mechanisms of competitive interactions between Barred and Northern Spotted Owls, and many of the variables identified as being important for Barred Owls in other parts of their range are strikingly similar to those found at Northern Spotted Owl sites in the Pacific Northwest. Barred Owls are known to be more generalist in habitat and diet than Northern Spotted Owls (Hamer et al., 2001). Known habitat associations suggest they are more abundant in productive forests and all the variables selected are associated with forest productivity on some level. I also assumed that the same factors which discriminated between Barred and Northern Spotted Owl centered sites would be important predictors of which Northern Spotted Owl sites will be occupied by Barred Owls.

To identify unexpected relationships between Barred Owl occupancy and measured habitat elements, I evaluated the entire set of predictor variables in an exploratory analysis for the two groupings of sites. I first tested all variables using univariate tests of significance at a conservative value of $p < 0.25$ to remain in the analysis (Hosmer and Lemeshow, 2000, p. 95). Histograms of continuous variables were visually inspected for normality, and log or arcsin transformed when necessary. I then checked for correlations among variables. Where variables were highly correlated ($r > 0.5$), I kept the variable that provided the most reasonable mechanism for discriminating between species, was relevant to managers, showed a consistent trend across analyses, and was most accurately measured. All combinations of remaining variables were run and AICc values compared with these earlier models. In comparing the Barred and Northern Spotted Owl centered sites, 10 variables remained after this initial data screening, which would have required comparing over 1000 models in an all possible subsets analysis. Instead, I selected the best model from among 15 including all combinations of the 4 remaining landscape-scale covariates, then added the remaining stand-level variables one at a time to the best model from this set for an additional 5 models.

Results

Comparison of Barred and Northern Spotted Owl activity centers

A priori analysis- Northern Spotted Owls were found in steeper and topographically drier sites than Barred Owls. Three models had considerable support ($\Delta AIC_c < 2$) and all included slope and elevation (Table 2.3). There was some evidence for the importance of elevation, which appeared in the second ranked model having nearly equal weight to the top model. Elevation and slope were inversely correlated with, and topographic moisture was positively correlated with, a site being occupied by Barred Owls (Table 2.4). Confidence intervals for the odds ratios of slope and topographic moisture did not overlap 1, providing additional evidence for their importance. The point estimates of odds ratios indicated that with each increase in slope of 10 degrees, a site was only 30% as likely to be a Barred Owl site. Similarly, each increase of 1 unit on the topographic moisture index (1: dry to 9: aquatic) corresponded to a greater than tenfold increase in the odds that a site was a Barred Owl site.

Exploratory analysis- Modeling individually significant (Table 2.5) and weakly correlated ($r<0.5$) variables produced a best ranked model that included disturbance history and density of deciduous trees, as well as slope and elevation (Table 2.6). Confidence intervals for odds ratios of slope, disturbance history, and density of deciduous trees did not include one, indicating that these factors were important for discriminating between Barred Owl and Northern Spotted Owl sites (Table 2.7). As in the first hypothesis driven analysis, models indicated that as elevation increased, the odds that a site was a Barred Owl site decreased, although confidence limits included 1.

Comparison of Northern Spotted Owl activity centers with and without Barred Owls

A priori analysis- Barred Owls were more likely to occupy Northern Spotted Owl sites that were less steep and at lower elevations (Table 2.8). Slope appeared in all competitive models, and had an odds ratio confidence interval excluding one. There was weaker evidence for an effect of elevation, with a confidence interval that included 1. The magnitude of the effects of slope and elevation were similar to that at Barred and Northern Spotted Owl centered sites. Although topographic moisture and distance to stream were in moderately competitive models ($\Delta AIC_c <\sim 2$), odds ratio confidence intervals for both variables broadly overlapped 1. In addition, coefficients for both were in the opposite direction from the relationship found between Barred and Northern Spotted Owl centered sites (Table 2.9).

Exploratory analysis- Models including four individually significant ($p< 0.25$) and uncorrelated ($r < 0.50$) variables indicated Barred Owls were more likely to occupy Northern Spotted Owl sites closer to the park boundary and with more level topography (Tables 2.10, 2.11, 2.12). Elevation was included with distance to park boundary and slope in a model with nearly equal weight to the best model ($\Delta AIC_c = 0.220$). There was little evidence for the importance of sapling density. Both elevation and sapling density had weak negative correlations with the probability that Barred Owls would be found at a site, and 95% confidence intervals included 1.

Discussion

The weight of evidence suggests that Barred Owls were most likely to occupy sites that were lower elevation, in moister topographic positions, and on more level terrain than Northern Spotted Owl sites. At sites that were known to have supported Northern Spotted Owls, steeper sites were less likely to have been occupied by Barred Owls. In both groupings of sites, there was weaker evidence that Barred Owls were less likely to occupy sites at higher elevations. This suggests that any effect of elevation is additive to a more consistent effect of slope.

Overall, when landscape scale factors were accounted for, there was virtually no evidence of any stand structural characteristics correlating with Barred Owl presence. Perhaps this was because of my narrow scope of inferences: extensive, mature, closed canopy forest. While studies in western Washington found that Barred Owls used younger forest on average than did Northern Spotted Owls, (Pearson and Livezy, 2003; Herter and Hicks, 2000), Buchanan, et al. (2004) did not find this relationship in eastern Washington. Because Barred Owls are fairly common in variety of younger managed and human dominated landscapes, expanding the scope of a study to include these areas would create a wider divergence of stand structural attributes between Barred and Northern Spotted Owls. However, it does not appear that any specific stand structure routinely used by Northern Spotted Owls in ONP would reduce the likelihood of Barred Owl occupancy.

In the Cascade Mountains of Washington, Barred owls were associated with moister sites at lower elevations (Buchanan, et al., 2004; Pearson and Livezy, 2003). My covariate of distance to water (defined as > 4th order streams as classified on a 1;100,000 USGS topographic map) was not a good predictor of Barred Owl presence in ONP, however Barred Owls were more likely to occupy sites that were in moister topographic positions. I cannot rule out the possibility that a more strictly defined covariate of distance to water, limited to distance from larger rivers and associated riparian vegetation, may have influenced Barred Owl distribution. Elevation did not classify Barred Owl sites as well as slope and topographic moisture, two variables which were highly correlated with elevation and with each other in ONP.

The exploratory analysis of individually significant and uncorrelated variables identified stand replacing disturbance in the last 250 years and the presence of deciduous trees as possible predictors of where Barred Owls will be found. Both of these factors are found most frequently in the floodplains of large rivers where Barred Owls are most abundant in ONP. Buchanan et al. (2004) also found basal area of hardwoods to be higher at Barred Owl sites than at Northern Spotted Owl sites in eastern Washington. History of stand-replacing disturbance was a useful predictor of which Northern Spotted Owl sites would be occupied by Barred Owls, but had less influence distinguishing between Barred and Northern Spotted Owl activity centers. Of the sites with stand replacing disturbance in the last 250 years, fire was the most recent disturbance at roughly equal proportions of Barred and Northern Spotted Owl sites, 58 and 50% respectively. Barred Owl sites ($N = 17$ with some disturbance) were more likely to have stand replacing events other than fire, including logging (1), windthrow (2), and fluvial activity (4). Seven of 46 Northern Spotted Owl sites were classified as uneven-aged old-growth with no obvious stand replacing disturbance history, compared to only one of 19 Barred Owl sites.

Within Northern Spotted Owl sites, distance to park boundary was the only variable which improved the fit of the exploratory model over the best *a priori* model. Again, due to the physiography of ONP, most of the broad river floodplains are near the park boundary, while higher and steeper sites are more likely to be in the interior of the park, making it difficult to separate boundary effects from other landscape scale factors. Because these correlations were established through exploratory analyses, they should be considered untested hypotheses.

These results must be viewed as a snapshot during an ongoing increase in Barred Owl populations. Barred Owls still appear to be increasing in number in ONP and broadening their niche as the highest quality habitat is filled. Many of the Northern Spotted Owl activity centers measured in this study have since been displaced by Barred Owls, and analysis of only current Northern Spotted Owl locations would probably yield different results. My goal was to identify factors that led to some of these sites being occupied by Barred Owls, so including unoccupied sites was unavoidable, but the mean values reported at these Northern Spotted Owl sites are unlikely to reflect the current distribution of this species. In the same way, Barred Owl habitat characteristics would be dependent on the time period analyzed. Until Barred Owl populations stabilize, habitat differences between sites used by Barred and Northern Spotted Owls can be expected to decrease.

Factors separating Barred and Northern Spotted Owls are likely to differ across the range of the Northern Spotted Owl, especially in areas with different management policies than ONP. This is the first investigation of Barred and Northern Spotted Owl habitat relationships in an area without a history of timber harvest. Relationships between the species should be easier to interpret here, due to the lack of other confounding changes in forest cover, but there may be interactions between these relationships and timber harvest that could increase the risk to Northern Spotted Owl sites, as hypothesized by Pearson and Livezy (2003).

This study suggests that greater elevation and slope, and lesser topographic moisture at a site are important environmental variables for identifying areas where Barred Owl occupancy is less likely. We speculate that the most likely refugia for Northern Spotted Owls from Barred Owl competition will be steep, high elevation, relatively dry sites, which are also suitable for Northern Spotted Owls. The long-term question is whether enough such places exist on the landscape to support a viable population of Northern Spotted Owls. The results of this study cannot be used to predict with any certainty where Barred Owls will not be found in the future, because they are continuing to occupy new areas each season. Knowing where Barred Owls are least likely to displace Northern Spotted Owls should allow managers to focus protection efforts on these sites, however there is no evidence that management of a given site for specific stand conditions will favor Northern Spotted Owls.

Table 2.1. Full set of variables considered for regression analyses, some derived from multiple measured variables.

Variable name	Description	Method
Elevation	Elevation of plot center point.	1:24,000 topo map
Disturbance	More than 10% of plot younger than 250 yrs due to disturbance (1), all older than 250 yrs (0).	Increment cores from a sample of trees
Slope	Avgerage % slope of vegetation points.	Clinometer
Bare	Average % bare ground at vegetation points.	Visual estimate
Groundcover	Average % groundcover at vegetation points, sum of forb, fern.and grass classes, can be > 100% due to overlap.	Visual estimate
Shrub cover	Avg. % shrub cover at vegetation points, sum of deciduous shrub, evergreen shrub, and conifer seedlings, can be > 100% due to overlap.	Visual estimate
Saplings/Ha	Trees/Ha > 1m high and less than 10 cm dbh	Strip transect
Coarse woody debris ($m^{3/}$ Ha)	Volume of downed wood > 10 cm diam. in decay classes 2 and 3.	Strip transect
Small tree density	Density/ha of live trees 10-29 cm dbh.	Circular plot
Medium tree density	Density/ha of live trees 30-79 cm dbh.	Circular plot
Large tree density	Density/ha of live trees ≥80 cm dbh.	Circular plot
Decadence	Basal area of live trees greater than 80 cm dbh with any of three decadence codes: large diam. branches, broken tops and/or multiple tops.	Circular plot
Deciduous	Live, deciduous trees/ha.	Circular plot
Snag BA	Basal area/ha of snags in decay class 2 and 3.	Circular plot
Road distance	Distance in m to nearest road	GIS, Arcview spatial join
Stream distance	Distance in m to nearest fourth order or larger stream or large lake.	GIS, hand calculated
CV of dbh	Coefficient of variation of dbh of all trees >10 cm in 10 m radius plot.	Circular plot
Canopy cover	% of 250 m radius buffer around plot center that has greater than 70% canopy cover	Remote sensing, Pacific Meridian Resources, 1997.
Topographic moisture	An index from 1 (dry) to 9 (aquatic) of topographic moisture, derived from plant associations.	Henderson et al., 1989, p. 437-438.
Boundary distance	Distance to park boundary	GIS, Arcview spatial join

Table 2.2. Variables included in *a priori* model selection.

Variable	Rationale
Elevation	Other studies, our observations, and declining forest productivity with elevation
Slope	Other studies, our observations, and lower forest productivity on steeper slopes
Topographic moisture	Most productive sites on a local scale, anecdotal observations of association with moist sites
Distance from streams	Carey and Johnson p345 streamsides had highest diversity small mammal communities

Table 2.3. *A priori* logistic regression models evaluated for comparison of Barred Owl and Spotted Owl sites in ONP. Models are sorted by Akaike weights.

Model	-2log L	k	AICc	ΔAICc	Akaike weight
Slope+topomoist	48.684	4	57.351	0.000	0.311
Elevation+slope+topomoist	46.525	5	57.542	0.191	0.282
Slope+topomoist+streamdist	48.197	5	59.214	1.863	0.122
Elevation+slope	50.737	4	59.404	2.053	0.111
Elevation+slope+topomoist+streamdist	46.52	6	59.968	2.618	0.084
Elevation+slope+streamdist	50.581	5	61.598	4.247	0.037
Slope	56.382	3	62.775	5.425	0.021
Elevation+topomoist	54.89	4	63.557	6.206	0.014
Slope+streamdist	56.186	4	64.853	7.502	0.007
Elevation+topomoist+streamdist	54.848	5	65.865	8.514	0.004
Topomoist	60.757	3	67.150	9.800	0.002
Topomoist+streamdist	59.202	4	67.869	10.518	0.002
Elevation	61.482	3	67.875	10.525	0.002
Elevation+streamdist	61.376	4	70.043	12.692	0.001
Streamdist	77.963	3	84.356	27.006	0.000

Table 2.4. Logistic regression coefficients and estimated odds ratios for *a priori* variables included in comparison of Barred Owl and Spotted Owl sites in ONP. Event is modeled as Barred Owl site, so positive coefficients and odds ratios >1 indicate positive correlation with a site being a Barred owl site. Estimates are from the best model in Table 3 including the covariate.

Variable	Units	Coeff.	ΔAICc	Odds ratio	95% CI lower	95% CI upper
Slope	10 deg.	-1.201	0	0.3	0.13	0.61
Topographic Moisture	1	2.401	0	11.03	1.91	101.43
Elevation	100m	-0.273	0.191	0.76	0.49	1.09
Dist. to stream	100m	-0.017	1.863	0.98	0.93	1.03

Table 2.5. Univariate tests of habitat characteristics at Barred Owl (N = 19) and Spotted Owl (N = 46) sites.

	Spotted Owl sites		Barred Owl sites		
	Mean	SE	Mean	SE	*P*
Elevation (m)	668	31.42	417	49.56	< 0.01
Topographic moisture	4.8	0.06	5.4	0.11	< 0.01
Slope (deg.)	25	1.30	12	2.24	< 0.01
Dist. to stream (m)	1,288	195.46	1,021	313.54	0.11
Dist. to ONP Bound. (m)	7,713	903.64	6,323	1,463.45	0.16
Dist. to road (m)	5,033	809.51	2,928	1,019.72	0.02
% closed canopy	86	1.39	86	1.67	0.66
% bare	52	3.21	36	6.22	0.02
% groundcover	20	3.13	59	9.36	< 0.01
% shrub cover	36	3.20	31	5.11	0.93
Trees >80 cm dbh/Ha	33	2.67	30	4.27	0.61
Trees 30-80 cm dbh/Ha	183	11.47	151	16.07	0.13
Trees 10-30 cm dbh/Ha	301	30.34	203	52.31	0.01
Saplings/Ha	628	122.41	330	99.80	0.04
Decid. trees/Ha	6	2.73	41	12.32	< 0.01
CWD vol/Ha	275	35.66	323	48.62	0.17
Snag BA	11	1.44	12	2.35	0.79
Decadent tree BA	1.5	0.26	2.0	0.42	0.22
CV of tree dbh	0.65	0.02	0.58	0.03	0.07
>10% < 250 yr old	0.50	0.07	0.89	0.07	0.01

Table 2.6. Exploratory model set for Barred and Spotted Owl centered sites.

Model	-2log L	k	AICc	ΔAICc	Akaike weight
Elevation+slope+disturbance history	46.034	5	57.051	0.000	0.319
Elevation+slope+deciduous	46.365	5	57.382	0.331	0.270
Elevation+slope	50.737	4	59.404	2.353	0.098
Elevation+slope+bounddist	49.090	5	60.107	3.056	0.069
Elevation+slope+decadent trees	49.992	5	61.009	3.958	0.044
Elevation+slope+streamdist	50.581	5	61.598	4.547	0.033
Elevation+slope+smalltree/saplings	50.586	5	61.603	4.552	0.033
Slope+bounddist	52.961	4	61.628	4.577	0.032
Elevation+slope+bare	50.666	5	61.683	4.632	0.031
Elevation+slope+bounddist+streamdist	48.972	6	62.420	5.369	0.022
Slope+streamdist+bounddist	51.566	5	62.583	5.532	0.020
Slope	56.382	3	62.775	5.724	0.018
Slope+streamdist	56.186	4	64.853	7.802	0.006
Elevation	61.482	3	67.875	10.824	0.001
Elevation+streamdist	61.376	4	70.043	12.992	0.000
Elevation+bounddist	61.461	4	70.128	13.077	0.000
Elevation+streamdist+bounddist	61.375	5	72.392	15.341	0.000
Bounddist	77.830	3	84.223	27.172	0.000
Streamdist	77.963	3	84.356	27.305	0.000
Streamdist+Bounddist	76.457	4	85.124	28.073	0.000

Table 2.7. Logistic regression coefficients and estimated odds ratios for exploratory variables included in comparison of Barred Owl and Spotted Owl sites in ONP. Event is modeled as Barred Owl site, so positive coefficients and odds ratios >1 indicate positive correlation with a site being a Barred owl site. Estimates are from the best model in Table 6 including the covariate.

Variable	Units	Coeff.	ΔAICc	Odds ratio	95% CI lower	95% CI upper
Elevation	100m	-0.246	0	0.78	0.51	1.13
Slope	10 deg.	-1.345	0	0.26	0.1	0.57
Disturbance	No/Yes	1.995	0	7.35	1.2	76.1
Deciduous trees	#/Ha	0.023	0.331	1.02	1	1.06
Decadent trees	m^2 BA/Ha	-0.179	3.958	0.84	0.52	1.24
Dist. to stream	100m	0.011	4.547	1.01	0.96	1.07
Bare ground	10%	-0.042	4.632	0.96	0.69	1.31
Dist. to ONP bound.	km	-0.08	15.341	0.93	0.81	1.04

Table 2.8. *A priori* logistic regression models evaluated for comparison of Spotted Owl sites with and without Barred Owl presence in ONP. Models are sorted by Akaike weights.

Model	-2log L	k	AICc	ΔAICc	Akaike weight
Elevation+slope	53.768	3	60.339	0.000	0.239
Slope	56.213	2	60.492	0.153	0.222
Elevation+slope+topomoist	53.348	4	62.324	1.984	0.089
Elevation+slope+streamdist	53.430	4	62.406	2.066	0.085
Slope+streamdist	56.177	3	62.748	2.409	0.072
Slope+topomoist	56.186	3	62.757	2.418	0.071
Elevation	58.488	2	62.767	2.428	0.071
Elevation+slope+topomoist+streamdist	52.637	5	64.137	3.798	0.036
Elevation+topomoist	58.261	3	64.832	4.493	0.025
Elevation+streamdist	58.399	3	64.970	4.631	0.024
Slope+topomoist+streamdist	56.130	4	65.106	4.766	0.022
Topomoist	61.564	2	65.843	5.504	0.015
Streamdist	61.572	2	65.851	5.512	0.015
Elevation+topomoist+streamdist	58.071	4	67.047	6.707	0.008
Topomoist+streamdist	61.553	3	68.124	7.785	0.005

Table 2.9. Logistic regression coefficients and estimated odds ratios for *a priori* variables included in comparison of Spotted Owl sites with and without Barred Owl presence in ONP. Event is modeled as Barred Owl presence, so positive coefficients and odds ratios >1 indicate positive correlation with a site having Barred Owls. Estimates are from the best model including the covariate.

Variable	Units	Coeff.	ΔAICc	Odds ratio	95% CI lower	95% CI upper
Elevation	100m	-0.240	0.000	0.787	0.565	1.061
Slope	10 deg.	-0.835	0.000	0.434	0.178	0.925
Topographic Moisture	1	-0.516	1.984	0.597	0.115	2.826
Dist. to stream	100m	0.015	2.066	1.015	0.964	1.07

Table 2.10. Univariate tests of habitat characteristics at Spotted Owl sites with Barred Owls present and absent.

	Barred Owl absent		Barred Owl present		*P*
	Mean	SE	Mean	SE	
Elevation	711.1	43.0	506.6	35.4	0.09
Topographic moisture	4.8	0.1	5.1	0.1	0.91
Slope	27.4	1.5	16.6	1.7	0.02
Dist. to stream	1,300.1	245.3	1,142.2	225.6	0.93
Dist. to Boundary	8,485.3	1,103.3	6,415.4	1,047.0	0.08
Dist. to road	5,980.9	1,115.4	3,234.5	730.5	0.08
% closed canopy	86.4	1.4	85.9	1.6	0.69
% bare	52.1	3.7	43.4	4.4	0.91
% groundcover	22.1	4.4	38.7	6.3	0.58
% shrub cover	34.2	3.5	34.6	4.0	0.59
Trees >80 cm dbh/Ha	35.1	3.5	29.9	2.9	0.30
Trees 30-80 cm dbh/Ha	181.0	12.9	168.3	13.6	0.83
Trees 10-30 cm dbh/Ha	285.4	40.6	261.9	35.9	0.50
Saplings/Ha	730.5	188.5	398.1	72.4	0.15
Decid. trees present	4.3	2.5	25.4	7.4	1.00
CWD vol/Ha	317.8	51.2	266.9	33.0	0.08
Snag BA	12.59	1.80	11.03	1.67	0.18
Decadent tree BA	1.51	0.37	1.81	0.28	0.68
CV of tree dbh	0.65	0.03	0.61	0.02	0.69
>10% < 250 yr old	0.43	0.10	0.76	0.07	0.37

Table 2.11. Exploratory model set for Spotted Owl sites with Barred Owls present and absent.

Model	-2log L	k	AICc	ΔAICc	Akaike weight
Slope+bounddist	50.675	4	59.651	0.000	0.302
Elevation+slope+bounddist	48.371	5	59.871	0.220	0.271
Slope+bounddist+sapden	50.267	5	61.767	2.116	0.105
Elevation+slope+bounddist+sapden	48.149	6	62.303	2.652	0.080
Elevation+slope	53.768	4	62.744	3.093	0.064
Slope	56.213	3	62.784	3.134	0.063
Slope+sapden	55.562	4	64.538	4.887	0.026
Elevation+slope+sapden	53.337	5	64.837	5.186	0.023
Elevation	58.488	3	65.059	5.409	0.020
Elevation+bounddist	57.353	4	66.329	6.678	0.011
Elevation+sapden	57.670	4	66.646	6.995	0.009
Sapden	60.321	3	66.892	7.242	0.008
Bounddist	60.375	3	66.946	7.296	0.008
Elevation+bounddist+sapden	56.504	5	68.004	8.353	0.005
Bounddist+sapden	59.039	4	68.015	8.364	0.005

Table 2.12. Coefficient values for exploratory model selection at Spotted Owl sites with and without Barred Owls.

Variable	Units	Coeff.	ΔAICc	Odds ratio	95% CI lower	95% CI upper
Slope	10 deg.	-1.370	0.000	0.254	0.083	0.624
Dist. to ONP bound.	km	-0.150	0.000	0.861	0.739	0.977
Elevation	100m	-0.243	0.220	0.785	0.556	1.072
Sapling density	100	-0.031	2.116	0.969	0.842	1.057

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Appendix 1- Comparison of year to year movement at Northern Spotted Owl sites relative to presence of Barred Owls

The analysis of Northern Spotted Owl site movement (p. 11) requires an assumption that the control sites (those without Barred Owls) did not move more or less than Northern Spotted Owl sites without Barred Owls for some reason other than Barred Owl presence. I tested whether the "control" sample of Northern Spotted Owl sites without Barred Owls exhibited similar year-to-year movement as the sites with Barred Owls prior to the first Barred Owl detection. I refer to this as year-to-year movement because it represented the mean distance an annual site center had shifted since the last year the site was occupied, even when more than one year passed between detections. I also tested for differences in movement at a site before and after Barred Owls were detected, conducting a paired t-test of the mean movement between the years that the site was occupied. This test evaluated the spatial stability of a Northern Spotted Owl site before and after Barred Owls, rather than the net movement as in the previous analysis.

There was no difference between the mean year-to-year movement of sites without Barred Owls ($N = 16$) and that at sites with Barred Owls prior to the first Barred Owl detection ($N = 26$) (426 m (230.6) and 483 m (241.8) respectively, $t_{40} = 0.747$, 2-tailed $p = 0.459$). There was no also no evidence for changes in the mean year-to-year movement of Northern Spotted Owl site centers before and after Barred Owls (mean (SD) distance 473 m (194.8) and 590 m (384.8) respectively, paired $t_{20} = 1.221$, 2-tailed $p = 0.236$). This suggests that the movements were generally a one-time shift in the Northern Spotted Owl activity correlating with the arrival of Barred Owls, after which the Northern Spotted Owls did not show a tendency to shift annual activity with any more frequency than before the arrival of Barred Owls.