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DISTRIBUTION, NUMBERS, AND SITE CHARACTERISTICS OF SPOTTED OWLS AND BARRED OWLS IN THE CASCADE MOUNTAINS OF WASHINGTON[1]

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ABSTRACT.—We analyzed distribution, numbers, and site characteristics of northern Spotted Owls (*Strix occidentalis caurina*) and northern Barred Owls (*Strix varia varia*) in Gifford Pinchot National Forest, Washington from July 1978–November 2001. Spotted Owl site-centers averaged significantly higher in elevation and in areas with steeper slopes than Barred Owl site-centers. Relative percentage of Barred Owl detections increased 8.6% annually during the study period. Plots of 0.8-km radius (201 ha) centered on Spotted and Barred owl sites differed significantly from random plots ($N = 500$); plots of both species contained more forest ≥180 yr old and fewer ha of forest 50–79 yr old, and Spotted Owl plots contained more forest 130–179 yr old. Spotted Owl site-centers were in significantly older forest than Barred Owl and random site-centers. Occupied Spotted Owl sites with timber harvest since 1978 contained significantly more forest ≥80 yr old than unoccupied sites with harvest. Occupancy of Spotted Owl sites in 2001 relative to number of Barred Owl sites, and slope and elevation of Spotted Owl sites, could be traced directly or indirectly to the presence of Barred Owls.

KEY WORDS: *northern Barred Owl*; Strix varia varia; *northern Spotted Owl*; Strix occidentalis caurina; *occupancy*; *site characteristics*; *Washington*; *Cascade Mountains*.

DISTRIBUCIÓN, NÚMEROS Y CARACTERÍSTICAS DE SITIOS DE *STRIX OCCIDENTALIS* Y *STRIX VARIA* EN LAS MONTAÑAS CASCADES DE WASHINGTON

RESUMEN.—Analizamos la distribución, los números, y las características de los sitios de *Strix occidentalis caurina*, considerados en peligro de extinción en los Estados Unidos, y de *Strix varia varia*, que están invadiendo el noroeste de los Estados Unidos. El área de estudio abarcó 217 812 ha en el Bosque Nacional Gifford Pinchot, Washington, y estudiamos estos búhos desde julio de 1978 a noviembre del 2001. En promedio, los sitios de *Strix occidentalis* estaban en lugares significativamente más altos en elevación y más inclinados que los de *Strix varia*. El porcentaje relativo de detecciones de *Strix varia* aumentó 8.6% al año. Los sitios de un radio de 0.8 km (201 ha) de *Strix occidentalis* y las de *Strix varia* difirieron de los sitios al azar ($N = 500$) porque los sitios de ambas especies tenían más áreas de bosques de por lo menos 180 años de edad y menos áreas de bosques de 50–79 años de edad, y los sitios de *Strix occidentalis* tenían más áreas de 130–179 años de edad. Los centros de los sitios de *Strix occidentalis* estaban situados en bosques más viejos que los de *Strix varia* y los de sitios al azar. Los sitios ocupados por *Strix occidentalis* con tala de árboles desde 1978 tenían más áreas de bosques de por lo menos 80 años de edad que los sitios inocupados con tala de árboles. La ocupación de los sitios de *Strix occidentalis*

[1] The views herein reflect those of the authors and are not necessarily those of the U.S. Fish and Wildlife Service.

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en 2001 en relación al número de los sitios de *Strix varia*, y la inclinación y elevación de los sitios de *Strix occidentalis*, puede estar directamente o indirectamente relacionada a la presencia de *Strix varia*.
[Traducción de Kent Livezey]

The northern Spotted Owl (*Strix occidentalis caurina*) is a resident of forest areas in southwestern British Columbia, western Washington and Oregon, and northwestern California. It was listed as a "threatened" subspecies in 1990, primarily due to evidence that the population was declining concurrent with loss of habitat (Federal Register 55:26 114–26 194, 26 June 1990, Gutiérrez 1994). The Barred Owl (*Strix varia*) was originally widespread throughout southeastern Canada, eastern United States, and eastern Mexico (Rignall 1973). In the early 1900s, the northern Barred Owl (*S. v. varia*) began to expand is range westward, moving across southern Canada and south into Washington, Oregon, and California. Barred Owls were first detected in Washington in 1965 (Rogers 1966), Oregon in 1974 (Taylor and Forsman 1976), and California in 1981 (Evens and LeValley 1982). The range of the Barred Owl now nearly completely overlaps that of the northern Spotted Owl. Barred Owls are larger than Spotted Owls, are aggressive toward them (e.g., Hamer et al. 1989, Leskiw and Gutiérrez 1998), and may compete with them (Hamer et al. 1989, Herter and Hicks 2000, Kelly et al. 2003).

Although a number of authors have suggested that Barred Owls compete with Spotted Owls, the range expansion of the Barred Owl is so recent that there have been only a few studies in which relationships between Barred Owls and Spotted Owls have been investigated (Hamer 1988, Hamer et al. 1989, 1994, 2001, Herter and Hicks 2000, Kelly 2001, Kelly et al. 2003). In this paper, we present data from a 24-yr study (1978–2001) during which we monitored the distribution, number, and habitat associations of Barred and Spotted owls in southwestern Washington. Our objectives were to: (1) describe temporal changes in the relative number and distribution of Barred and Spotted owls; (2) compare habitats occupied by both species, and (3) evaluate occupancy of territories by Spotted Owls as a function of the presence or absence of Barred Owls.

METHODS

Study Area. The study area was the Cowlitz Valley Ranger District of the Gifford Pinchot National Forest (GPNF). This 217 812-ha area was located on the west slope of the Cascade Mountains in southwestern Washington (Fig. 1). Forested vegetation on the study area was dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*), subalpine fir (*Abies lasiocarpa*), and western redcedar (*Thuja plicata*). Small, local areas of deciduous hardwoods (1146 ha), such as bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*), were mostly in riparian areas.

Figure 1. Location of study area (shaded area) in southern Washington.

Much of the study area exhibited the effects of large-scale fires, resulting in large blocks of contiguous forest of the same general age. Forest harvest began in the study area in about 1947. By 2001, forested areas 50–129 yr old were still relatively untouched by timber harvest, whereas forested areas ≥130 yr old either were heavily fragmented by logging outside of wilderness or remained in contiguous blocks within wilderness. In some areas, older forest was found in narrow bands along valley bottoms, intergrading into younger forest on upper slopes and ridges. The four main forest zones in the study area, with approximate elevation limits, were western hemlock (<914 m), Pacific silver fir (914–1373 m), mountain hemlock (1372–1708 m), and subalpine fir (1707 m-treeline) (GPNF unpubl. data). The Douglas-fir, a pioneer species that repopulates areas denuded by forest fire, was present throughout the study area within all four forest zones. In addition, old-growth Douglas-fir were present throughout the study area as remnants left after forest fires. In 2001, the study area was composed of ca. 52% forest ≥80 yr old, 33% forest <80 yr old, and 15% non-

forested areas (rock, wet-mesic, dry meadow/brush, water). The study area contained ca. 2630 km of roads.

The Northwest Forest Plan (USDA and USDI 1994a, 1994b) placed every ha of federally-administered land within the range of the northern Spotted Owl into one of many land-use allocations (LUAs). Within the study area, the LUAs in which timber harvest was permitted were matrix (49 716 ha) and an adaptive management area (42 741 ha), and the LUAs in which no timber harvest was permitted were late-successional reserves (55 275 ha), congressionally-reserved areas (42 721 ha), and administratively-withdrawn areas (27 359 ha). The Northwest Forest Plan permits certain forest activities in late-successional reserves, such as thinning in stands ≤80 yr old, when they are beneficial to the creation of late-successional forest characteristics. Critical habitat units (Federal Register 57:1796–1838 15 Jan 1992) (81 597 ha) overlaid all other LUAs except congressionally-reserved areas; timber harvest was permitted in critical habitat if it overlaid an adaptive management area or matrix.

Survey Methods. Spotted and Barred owls respond to imitations of their calls, and Barred Owls readily respond to Spotted Owl calls (Forsman et al. 1984, McGarigal and Fraser 1985, Hamer 1988, Reid et al. 1999). Amplified tape recordings or voice imitations of Spotted Owl calls were used to detect Spotted Owls and Barred Owls. Hybrid Spotted × Barred owls were identified by their distinctive five- or six-note calls that are "strikingly different" from Spotted Owl four-note calls and Barred Owl eight-note calls (Hamer et al. 1994). Surveys followed accepted protocols (Forsman 1983). Spotted Owl habitat was identified within each survey area and survey stations were located to achieve complete coverage of the habitat. Survey stations were 0.2–0.8 km apart within Spotted Owl habitat, typically along roads. Each survey was conducted for at least 10 min per station unless a Spotted Owl, Barred Owl, or Great Horned Owl (*Bubo virginianus*) was detected, in which case calling was stopped to minimize disturbance to Spotted Owls and potential confrontations between owl species.

Survey effort varied from year to year. Forest Service surveys were conducted according to several region-wide survey programs, including random-area surveys and surveys surrounding proposed timber sales, targeting portions of the entire study area each year with no single year achieving total coverage. However, by 1992, the entire study area had been surveyed cumulatively. From 1994–2001, R. Pearson achieved nearly complete coverage in even years and in 2001, while the other years had partial coverage. Because of this, our total sites for Spotted and Barred owls represent cumulative totals rather than the total in 2001.

Data Analysis. In our analysis, a Spotted or Barred owl "site" was analogous to an individual owl territory. Sites were designated based on the presence of nests, fledged young, or repeated detections of paired or single owls in the same general area. Resident single sites required ≥ three detections of a male or female owl on three different survey outings. Pair sites required ≥ one detection of both a male and a female that was >1.6 km from a known site for Spotted Owls and >0.8 km from a known site for Barred Owls. The 1.6-km requirement for Spotted Owl sites was waived in one instance when a new pair site with fledglings was identified <1.6 km from two known sites, and adults of the adjacent pairs were also detected.

For Barred Owls, we also used a category called "potential sites" that included suspected territories that were based on one or two detections of a single owl in an area that was ≥0.8 km from any other Barred Owl sites. The 0.8-km cutoff for designation of potential sites was based on Hamer et al. (1989), who reported a 218-ha mean summer home-range for Barred Owls (a circular plot of 0.8-km radius includes 201 ha). For each site, we plotted a "site-center" based on the location of the nest tree, fledged young, multiple detections of a pair, or multiple detections of single owls. For Spotted Owl pairs that changed nest trees or centers of activity within sites, we used the most recent locations to plot site-centers. For comparison of forest-stand age at the site-center, we identified the age of the forest stand that included the site-center. We considered Spotted Owl sites unoccupied if they were occupied by a pair for ≥1 yr, and were subsequently surveyed ≥10 times during the last 5 yr of the study (1997–2001) with no detections of Spotted Owls within a 1.6-km radius. We excluded sites that were not surveyed ≥10 times during the last 5 yr of the study (N = 16) from analyses of Spotted Owl site occupancy. We analyzed landscape attributes around site-centers based on comparisons of vegetation composition within a 0.8-km radius centered on the owl site-centers and random locations, which we called "core-plots" (Hunter et al. 1995, Meyer et al. 1998, Swindle et al. 1999, Herter and Hicks 2000, Kelly 2001). We centered random sites on the first 500 randomly generated, terrestrial locations below 1524 m in elevation. We excluded random locations above 1524 m elevation because we detected no Spotted or Barred owls above 1524 m, and excluded non-forested areas (rock, wet-mesic, dry meadow/brush, and water) from vegetation analyses. To approximate Spotted Owl home ranges in Fig. 2, we used a 2.9-km radius circle (2670 ha) following Herter and Hicks (2000). For each owl site, we determined a "nearest-neighbor distance" which was the distance to the nearest known site-center of the same species (Hamer et al. 1989, Anthony 2001). We estimated the "minimum nearest-neighbor distance" for Spotted Owls by measuring the distance to the nearest nest trees being used by adjacent pairs in the same year. We found no Barred Owl nest trees, so for this species we estimated minimum nearest-neighbor distance by taking the mean of the 10 shortest distances between Barred Owl site-centers.

We used ArcView version 3.1.1 (Environmental Systems Research Institute, Inc., Redlands, CA) to analyze spatially geographic, physiographic, vegetation, and owl data. GPNF geographic information system database supplied basic forest-age data. We divided the forested area into five age groups, as follows: 0–49-yr-old forest (mainly young trees growing on harvested areas); 50–79-yr-old forest (natural stands growing in burned areas without any late-successional characteristics); 80–129-yr-old forest (forest developing late-successional characteristics); 130–179-yr-old forest (an equal sub-division between forest ≥80 yr old and forest <180 yr old to test for potential differences of younger and older mature forest); and forest ≥180 yr old (forest with late-successional characteristics). In western Washington, Douglas-fir stands usually begin to develop late-successional characteristics by the

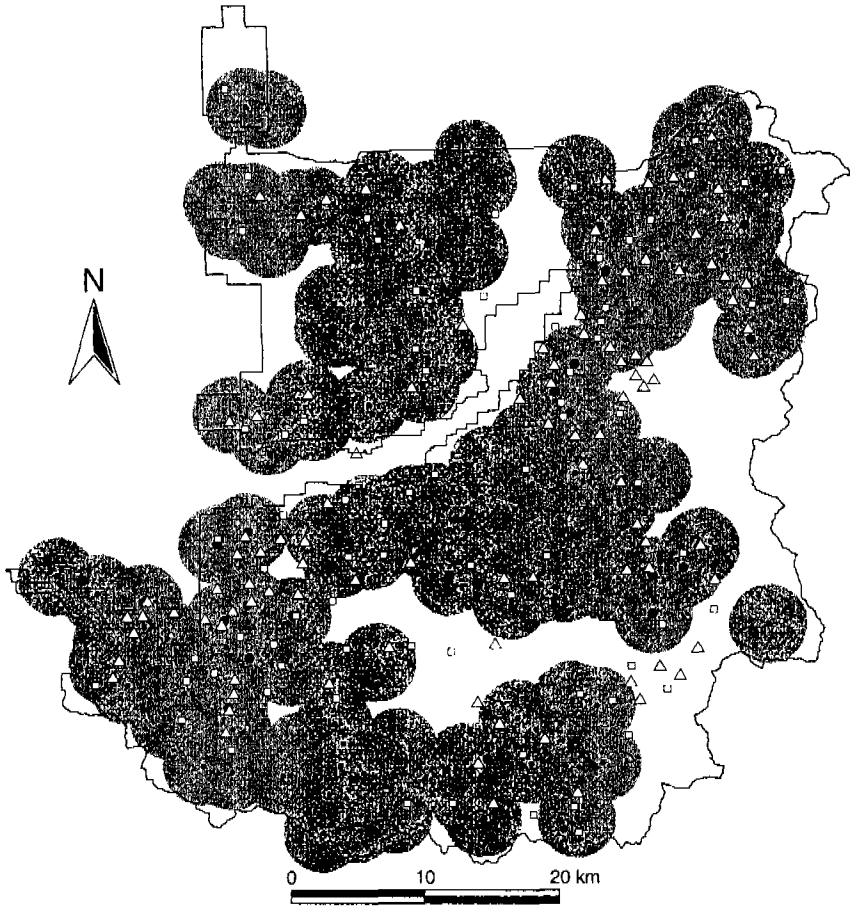

Figure 2. Locations of Spotted Owl occupied sites (N = 120, small dots), Spotted Owl unoccupied sites (N = 25, large dots), Barred Owl sites (N = 98, triangles), and potential Barred Owl sites (N = 76, boxes). Gray circles represent Spotted Owl home-range circles of 2.9-km radius.

time they are ≥80 yr old, including relatively large live and dead trees with some multi-layered canopies, and some large woody debris on the forest floor (USDA and USDI 1994a). We estimated the 1946 forest-age throughout the study area by subtracting 55 yr from the age in 2001 of each forested area. For areas where the 2001 forest-age was <55 yr, such as clearcut and burned areas, we estimated an original yr of origin based upon surrounding forest (e.g., a clearcut surrounded by forest with a 1729 yr-of-origin was given the same yr-of-origin) and then subtracted 55 yrs.

We used nonparametric statistical tests because most of our data did not fit a normal distribution. Statistical tests (two-tailed Mann-Whitney U-test, Spearman coefficient of rank correlation) were carried out using SYSTAT Version 10 (SPSS Inc., Chicago, IL). We followed Sokal and Rohlf (2000) to calculate χ^2 tests. Significance level for all tests was α = 0.05. Sample sizes in statistical tests were presented only when they departed from N = 500 for random sites, N = 145 for Spotted Owl sites and N = 98 for Barred Owl sites. All means were expressed as $x \pm 1$ SD.

For comparison of aspect between random, Spotted and Barred owl site-centers, we conducted chi-square tests of the frequency of site-centers within each of four directions (northeast, southeast, southwest, and northwest), north vs. south, and east vs. west, and we included only those random points that were in forest stands ≥80 yr old (N = 250) to ensure that results would indicate possible selection rather than availability. Aspects for random site-centers were not equally distributed in each of the four directions due to naturally occurring differences in the landscape.

We examined change in percentage of Barred Owl detections relative to all *Strix* detections. For this analysis, we determined the first and last years to be included in our sample of owl detections over time as follows: (1) we started with 1982 because it was the first yr with ≥25 total *Strix* detections, and (2) we ended with 2000 because sur-

Table 1. Mean (±SD) elevation (m) and slope (%) of Spotted Owl, Barred Owl, and random site-centers in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.[a]

	SPOTTED OWL (N = 145)	BARRED OWL (N = 98)	RANDOM (N = 500)
Elevation	966.2 ± 197.2[b,c]	812.5 ± 275.9[b,d]	1070.3 ± 282.6[c,d]
Slope	54.1 ± 14.5[b,c]	39.2 ± 18.6[b,d]	46.2 ± 17.16[c,d]

[a] All significant Mann-Whitney P-values < 0.001.
[b] Mean differed from random site-centers.
[c] Mean differed from Barred Owl site-centers.
[d] Mean differed from Spotted Owl site-centers.

veys in 2001 emphasized detecting Barred Owls more than in previous years. Because there were no Barred Owl detections in 1982, but there were Barred Owl detections in previous and in later years, we estimated the 1982 Barred Owl percentage as the mean of the detections for this species for the 9 yr centered on 1982 (1978—86). We were unable to test the effect of Barred Owl presence on Spotted Owl site occupancy in sites that had not been harvested due to small sample sizes.

RESULTS

Total Detections and Sites. We recorded 2170 Spotted Owl and 521 Barred Owl detections during July 1978–November 2001. Based on these detections, we identified 145 Spotted Owl sites, 98 Barred Owl sites, and 76 potential Barred Owl sites in the study area (Fig. 2). Spotted Owl sites were centered on nests (N = 43), young (N = 41), locations of adults of both sexes detected at the same time (N = 44), locations of adults of both sexes detected at different times (N = 11), and resident singles (N = 6). Barred Owl sites were centered on young (N = 8), locations of adults of both sexes detected at the same time (N = 51), locations of adults of both sexes detected at different times (N = 21), and resident singles (N = 18). We believe we found virtually all of the Spotted Owl sites in the study area sometime during 1978–2001, and that the actual total number of Barred Owl pair sites in our study area was probably closer to our total (N = 174) for both the Barred Owl sites and the potential Barred Owl sites.

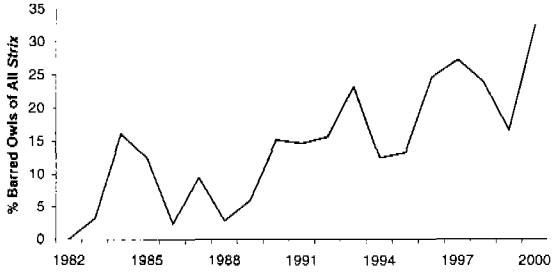

Figure 3. Percent of Barred Owl detections relative to all *Strix* detections by year, 1982–2000.

Distribution and Numbers. Both Spotted and Barred owl site-centers were significantly lower in elevation than random, and Spotted Owl site-centers were significantly higher in elevation than Barred Owl site-centers (Table 1). Spotted Owl site-centers were situated in areas of significantly steeper slope than random and Barred Owl site-centers. Barred Owl site-centers were situated in areas of significantly less slope than random. None of the tests of aspect showed any significant difference between Spotted Owl, Barred Owl, and random site-centers for the four directions (χ^2_3 = 1.63–5.99, P > 0.10) or for north vs. south or east vs. west (χ^2_1 = 0.30–3.30, P > 0.05).

Table 2. Mean (±SD) area (ha) of five forest-age classes within 0.8-km radius plots (201 ha) around Spotted Owl, Barred Owl, and random site-centers in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.[a]

FOREST-AGE CLASS (yr)	SPOTTED OWL (N = 145)	BARRED OWL (N = 98)	RANDOM (N = 500)
0–49	47.9 ± 32.1[b]	42.8 ± 33.0	43.5 ± 42.8[c]
50–79	10.8 ± 26.3[b]	12.2 ± 33.6[b]	28.8 ± 52.4[c,d]
80–129	28.8 ± 42.2	32.3 ± 45.8	35.0 ± 51.2
130–179	17.2 ± 31.2[b]	14.2 ± 30.2	10.7 ± 24.7[c]
≥180	82.4 ± 44.6[b]	84.6 ± 54.1[b]	57.1 ± 49.6[c,d]

[a] Significant Mann-Whitney P-values ranged from P < 0.02 to P < 0.001. None of the means differed between Spotted Owl and Barred Owl sites (all Mann-Whitney P-values > 0.20).
[b] Mean differed from random core-plots.
[c] Mean differed from Spotted Owl core-plots.
[d] Mean differed from Barred Owl core-plots.

Table 3. Age of forest stand at site-centers of Spotted Owl, Barred Owl, and random sites in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.

Forest-age Class (yr)	Study Area		Spotted Owl (N = 145)		Barred Owl (N = 98)		Random (N = 442)[a]	
	Ha	%	No.	%	No.	%	No.	%
0–49	41 951	24.1	0	0	1[b]	1.0	111	25.1
50–79	28 193	16.2	1	0.7	4	4.1	78	17.6
80–129	34 934	20.1	15	10.3	19	19.4	89	20.1
130–179	11 814	6.8	10	6.9	7	7.1	26	5.9
≥180	57 252	32.9	119	82.1	67	68.4	138	31.2
Total	174 144		145		98		442[b]	

[a] The 58 random site-centers that fell in non-forested areas (rock, wet-mesic, dry meadow/brush) were excluded from this analysis.
[b] A 42-yr-old clearcut that retained some remnant old-growth trees.

The percent of Barred Owl detections (N = 403) relative to all *Strix* detections (N = 2431) increased significantly annually from 1982–2000 (r_s = 0.790, $P < 0.001$, N = 19). Overall, Barred Owl detections increased 8.6% annually from 1982–2000, and there did not appear to be any leveling-off of this increase (Fig. 3). Thirty-three percent (78 of 240) of the *Strix* detections in 2000 were Barred Owl detections, and 53% (113 of 215) of the *Strix* detections in 2001 (when detecting Barred Owls was emphasized) were Barred Owl detections. The minimum nearest-neighbor distances for Barred Owls and Spotted Owls were 1.1 km and 1.6 km, respectively.

Hybrids. We detected two hybrids between Spotted and Barred owls. The first, which had a distinctive five-note call, was detected once in 1994 and not afterward. The second hybrid, which had a distinctive six-note call, was audibly detected annually from 1995–2000.

Site Characteristics. Spotted and Barred owl sites did not differ relative to the amount of different forest-age classes within core-plots (Table 2). On average, core-circles of both species contained more forest ≥180 yr old and less forest 50–79 yr old than random plots. Spotted Owl plots also contained more 130–179-yr-old forest and 0–49-yr-old forest than random plots.

Number of Spotted Owl site-centers in each forest-age group differed from Barred Owls (χ^2_4 = 9.61, $P < 0.05$) and random (χ^2_4 = 130.31, $P < 0.001$), and that of Barred Owl site-centers differed from random (χ^2_4 = 61.56, $P < 0.001$; Table 3). Mean age of forest stand at site-centers was significantly greater (U = 5844.5, $P < 0.02$) for Spotted Owls (254.7 ± 76.5 yr) than for Barred Owls (228.3 ± 101.5 yr). Thirty-three percent of forest in the study area was comprised of stands ≥180 yr old, and 28% of random site-centers were in these old-forest stands. However, 82% of Spotted Owl and 68% of Barred Owl site-centers were in these old-forest stands (Table 3).

Site Occupancy. Of the 129 Spotted Owl sites with ≥10 surveys during the last 5 yr of the study, 25 (19.4%) apparently were unoccupied by Spotted Owls by 2001. There were significantly more

Table 4. Mean (±SD) elevation (m) and slope (%) of occupied and unoccupied Spotted Owl site-centers and Barred Owl site-centers in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.[a]

	Occupied Spotted Owl (N = 104)	Unoccupied Spotted Owl (N = 25)	Barred Owl (N = 98)
Elevation	982.9 ± 143.9[b]	886.4 ± 291.8	812.5 ± 275.9[d]
Slope	57.1 ± 12.1[b,c]	43.0 ± 19.2[d]	39.2 ± 18.6[d]

[a] All significant Mann-Whitney P-values < 0.001.
[b] Mean differed from Barred Owl site-centers.
[c] Mean differed from unoccupied Spotted Owl site-centers.
[d] Mean differed from occupied Spotted Owl site-centers.

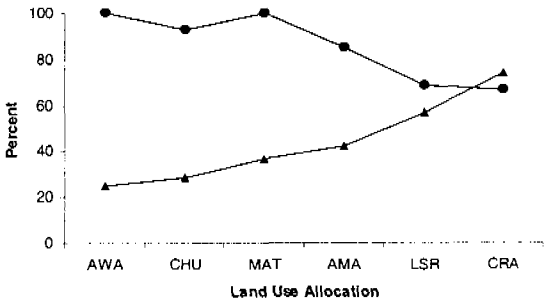

Figure 4. The percent of Spotted Owl sites that were occupied (circles) compared to the percent of Barred Owl sites relative to all occupied *Strix* sites (triangles) by Land Use Allocation. Timber harvest was permitted in critical habitat units (CHU), matrix (MAT), and the adaptive management area (AMA), and was not permitted in administratively-withdrawn areas (AWA), late-successional reserves (LSR), and congressionally-reserved areas (CRA).

Table 5. Reserve areas and timber harvest relative to number of occupied Spotted Owl sites ($N = 104$), Barred Owl sites, and all Barred Owl (including potential Barred Owl sites) sites ($N = 174$) in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.

			Timber Management	
	Critical Habitat	Late Successional Reserve	No Harvest[a]	Harvest Permitted[b]
Spotted Owl sites	57	35	44	60
Barred Owl sites	55	47	64	34
All Barred Owl sites	89	73	102	72

[a] Includes late-successional reserve, congressionally-reserved areas, and administratively-withdrawn areas.

[b] Includes matrix and adaptive management area.

Barred Owl site-centers in: (1) unoccupied (0.44 ± 0.51) than occupied (0.14 ± 0.35) Spotted Owl circles of 0.8-km radius ($U = 915.5$, $P = 0.001$), (2) unoccupied (0.84 ± 0.99) than occupied (0.44 ± 0.69) Spotted Owl circles of 1.6-km radius ($U = 1016.0$, $P = 0.049$), and (3) unoccupied (2.40 ± 1.83) than occupied (1.32 ± 1.38) Spotted Owl home-range circles of 2.9-km radius ($U = 845.5$, $P = 0.005$).

Occupied Spotted Owl sites were significantly steeper in slope and were significantly higher in elevation than Barred Owl sites (Table 4). Compared to unoccupied Spotted Owl sites, occupied Spotted Owl sites were also significantly steeper in slope, but were not significantly different in elevation. Unoccupied Spotted Owl sites were not significantly different than Barred Owl sites in slope or elevation.

The number of ha of forest ≥80 yr old was not significantly different in occupied (130.1 ± 36.3 ha) vs. unoccupied (123.4 ± 37.8 ha) ($U = 1445.0$, $P = 0.388$) Spotted Owl core-plots. However, when considering core-plots in which some forest harvest had taken place from 1978–2001 (20.6 ± 16.2 ha, range = 0.1–72.6 ha), occupied sites (125.5 ± 31.4 ha, $N = 83$) had significantly more forest ≥80 yr old than unoccupied sites (109.9 ± 28.6 ha, $N = 19$) ($U = 1022.0$, $P = 0.045$).

The percent of Spotted Owl sites that were occupied in each LUA was inversely proportional to the percent of Barred Owl sites relative to all occupied *Strix* sites ($r_s = -0.899$, $P < 0.01$, $N = 6$; Fig. 4). In areas specifically allocated to benefit Spotted Owls (critical habitat units and late-successional reserves), the number of Barred Owl sites approached or surpassed the number of occupied Spotted Owl sites (Table 5). The numbers of occupied Spotted Owl sites and Barred Owl sites differed between areas in which timber harvest was permitted and was not permitted ($\chi^2_1 = 10.77$, $P < 0.005$). There were more Spotted Owl sites than Barred Owl sites in areas with timber harvest and fewer Spotted Owl sites than Barred Owl sites in areas without timber harvest. When including potential Barred Owl sites, there were more than twice as many Barred Owl sites than Spotted Owl sites in areas without timber harvest, whereas in areas with timber harvest, there were slightly more Barred Owl sites than Spotted Owl sites (Table 5).

Discussion

Distribution and Numbers. Within the study area, more gradual slopes were along valley-bottoms and, in some cases, higher-elevation plateaus. Barred Owls generally appeared to favor the less-steep valley bottoms, while Spotted Owls were found more often in the steeper upland areas, a distinction also noted by Herter and Hicks (2000). Our analysis did not show that aspect had any influence on site selection by Spotted or Barred owls. Although studies in comparatively warmer regions of California indicated that Spotted Owls may select roosts or nests on north aspects during summer (Barrows 1981, North et al. 2000), studies in the more mesic conditions typical of western

Table 6. Mean (±SD) area (ha) of five forest-age classes in 0.8-km radius plots (201 ha) around 1946 Spotted Owl, 2001 Spotted Owl, 1946 random, and 2001 random site-centers in the Cowlitz Valley Ranger District, Gifford Pinchot National Forest, Washington.[a]

FOREST-AGE CLASS (yrs)	1946 SPOTTED OWL (N = 145)	2001 SPOTTED OWL (N = 145)	1946 RANDOM (N = 500)	2001 RANDOM (N = 500)
0–49	22.4 ± 39.3[c,d,e]	47.9 ± 32.1[b,e]	46.8 ± 63.9[b,e]	43.5 ± 42.8[b,c,d]
50–79	18.9 ± 38.2	10.8 ± 26.3[c]	21.7 ± 45.9[c]	8.8 ± 52.4[c,d]
80–129	17.5 ± 33.0[c,d]	28.8 ± 42.4[b]	10.3 ± 24.5[b,e]	35.0 ± 51.2[d]
130–179	22.0 ± 43.5	17.2 ± 31.2[e]	16.2 ± 34.6	10.7 ± 24.7[e]
≥180	106.1 ± 59.6[c,d]	82.4 ± 44.6[b,e]	80.2 ± 70.5[b]	57.1 ± 49.6[c,d]

[a] Significant Mann-Whitney P-values ranged from $P < 0.020$ to $P < 0.001$.
[b] Mean differed from 1946 Spotted Owl core-plots.
[c] Mean differed from 2001 Spotted Owl core-plots.
[d] Mean differed from 1946 random core-plots.
[e] Mean differed from 2001 random core-plots.

Oregon and Washington indicated little selection for aspect by Spotted Owls (Forsman et al. 1984, this study).

At the northern edge of the range of the Spotted Owl, surveys suggested that there were four times as many Barred Owl sites than Spotted Owl sites both in British Columbia during the late 1980s (Dunbar et al. 1991) and in North Cascades National Park, Washington, during 1993–96 (R. Kuntz and R. Christopherson unpubl. data). Hamer et al. (1989) found that Barred Owls were twice as abundant as Spotted Owls in the northern Cascade Mountains east of Mt. Baker in the late 1980s. Barred Owls were almost as numerous as Spotted Owls in the mid 1990s just north of Mt. Rainier (Herter and Hicks 2000) and, in our study area, it appeared that they were at least as numerous as Spotted Owls in 2001.

Our shorter minimum nearest-neighbor distance for Barred Owls vs. Spotted Owls, which also was found by Hamer et al. (1989), could be a result of the wider variety of prey that Barred Owls use (Hamer et al. 2001), thereby allowing Barred Owls to "pack" closer together. The shortest nearest-neighbor distance for Spotted Owls (1.6 km) in Forsman et al. (1984) was equal to our shortest nearest-neighbor distance.

Hybrids. Apparently, Spotted × Barred owl hybrids are rare. Kelly (2001) gathered reports of visual sightings of only 24 adult and 26 juvenile Spotted × Barred owl hybrids in Washington and Oregon from 1974–99.

Site Characteristics. Our data suggest that Spotted Owl site-centers were more often in older forest than Barred Owl and random site-centers. Also, territories of Spotted and Barred owls tended to be centered in areas characterized by higher concentrations of old forest and lower concentrations of 50–79-yr-old forest than were available at random. These findings were in agreement with most previous studies of Spotted Owls (Bart and Forsman 1992, Hunter et al. 1995, Swindle et al. 1999), but the similarity of forest age in Spotted and Barred owl core-plots was a somewhat surprising result. Barred Owls have been thought to be more habitat generalists than Spotted Owls (Hamer et al. 1989, Herter and Hicks 2000, Hamer et al. 2001), and seem to use much more varied habitats throughout the Pacific Northwest (Smith et al. 1997, Kelly and Forsman 2003). However, in the eastern United States and eastern Canada, Barred Owls are considered an old-growth forest species (Dunstan and Sample 1972, Devereux and Mosher 1984, Elody and Sloan 1985, Laidig and Dobkin 1995) and, in some areas, Barred Owls do not breed in or defend territories in younger forests (Haney 1997). In Manitoba, Barred Owl plots contained fewer clearcut, burned, and young forest areas than random plots, and were associated more with areas of high crown-closure than random plots (Hinam and Duncan 2002). Because Barred Owls use forests that are similar to those used by Spotted Owls in our study area, this may make it difficult to manage forests to benefit Spotted Owls over Barred Owls.

Spotted Owl core-plots in our study area contained more old forest (≥130 yr) than random sites, but contained less forest 50–79 yr old than

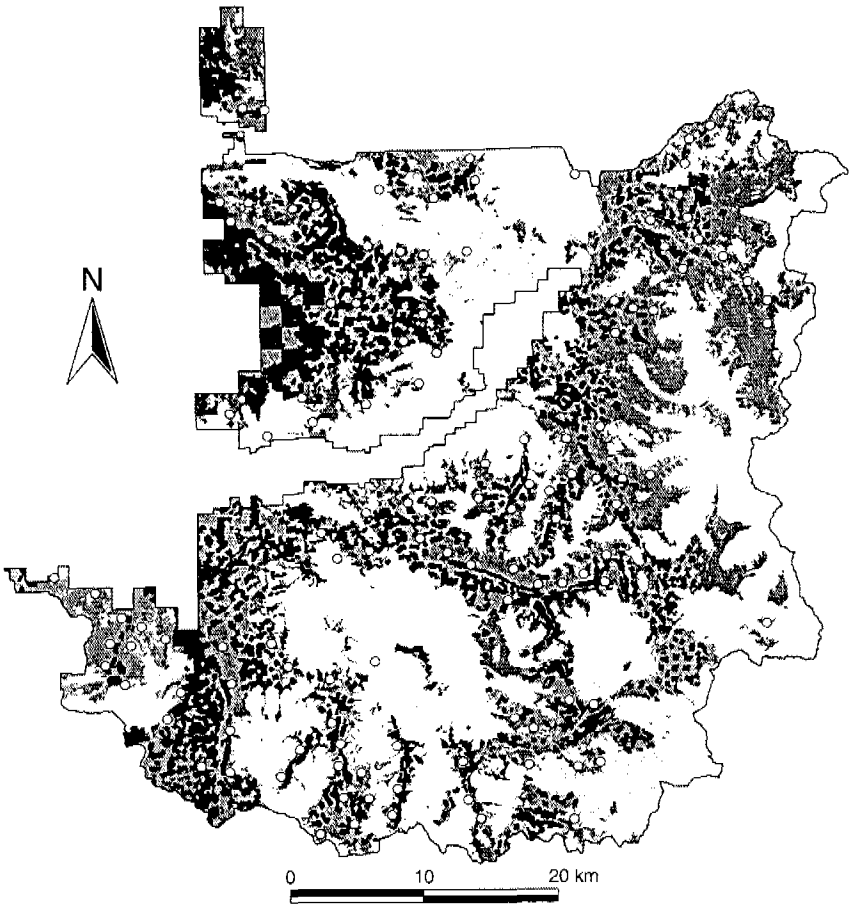

Figure 5. Forest ≥80 yr old in 1946 that was lost to forest harvest by 2001 (black areas), forest ≥80 yr old that remained in 2001 (dark gray areas), forest that became 80 yr old from 1946–2001 (light gray areas), and the 145 Spotted Owl site-centers (circles).

random. This finding, coupled with results from other studies that Spotted Owls are an old-forest associated species (USDA and USDI 1994a, 1994b), could lead to an expectation that Spotted Owl core-plots should contain less forest 0–49 yr old than random areas. However, Spotted Owl core-plots in our study area contained significantly more ha of 0–49-yr-old forest than random plots. To further examine this counter-intuitive result, we adjusted stand age to approximate the forest in the study area before any forest harvest took place (in 1946) to compare the forest-age distribution in Spotted Owl and random sites in 1946 vs. 2001 (Table 6). Spotted Owl core-plots in 1946 contained significantly less 0–49-yr-old forest than 1946 random sites, with a mean less than one-half that of random (22.8 vs. 46.8 ha). In 1946, the 0–49-yr-old forest was consolidated into large, contiguous areas caused by forest fires in the early 1900s, while in 2001, 0–49-yr-old forest, the result of thousands of clearcuts, was widely distributed and was intermixed with older forest. The distribution of Spotted Owl sites in 2001 mirrored very closely the distribution of forest ≥80 yr old in 1946, excluding the areas lost to forest harvest. Spotted Owls appeared to have persisted in areas of older forest. Other than a few instances, Spotted Owls had yet to repopulate the areas that had grown into forest ≥80 yr old by 2001 (Fig. 5).

Spotted Owl core-plots in our study area included more forest ≥130 yr old than random, but did not contain more forest 80–129 yr old than ran-

dom. However, forest practices reduced the amount of forest ≥130 yr old by 25 921 ha and increased the amount of forest 80–129 yr old by 22 672 ha. Replacing stands ≥130 yr old with stands 80–129 yr old could negatively affect Spotted Owls.

Our results were similar to previous studies in that Barred Owls were most abundant in lowland forests and less common in upland areas (Laidig and Dobkin 1995, Haney 1997, Mazur et al. 1997, Hamer 1988, Mazur et al. 1998). However, these owls also occurred in upland areas, as has been reported in previous studies (Boxall and Stepney 1982, Dunbar et al. 1991, Dark et al. 1998, Wright and Hayward 1998). Collectively, these results suggest that riparian zones and lowland forests were more suitable habitat for Barred Owls in our study area, and that upland forests were less likely to be occupied by Barred Owls.

The large standard deviations for elevation and slope (Table 1) indicated considerable variation among sites occupied by both Barred Owls and Spotted Owls. For example, there were four cases where Spotted Owl core-plots were dominated by 50–79-yr-old forest (53–96% cover), with only small areas of old forest or remnant older trees remaining.

Site Occupancy. When we analyzed only those core-plots in which some timber harvest had taken place since 1978, unoccupied Spotted Owl sites had significantly less forest ≥80 yr old remaining than occupied sites, indicating that forest harvest contributed to these sites becoming unoccupied. Occupancy of Spotted Owl sites, relative to (1) number of Barred Owl sites within Spotted Owl plots, (2) slope of Spotted Owl sites, and (3) elevation of Spotted Owl sites could be directly or indirectly traced to the presence of Barred Owls. There were significantly more Barred Owl sites within 0.8-km, 1.6-km, and 2.9-km radius circles centered on Spotted Owl site-centers in unoccupied Spotted Owl sites than in occupied Spotted Owl sites. Occupied Spotted Owl sites were on significantly steeper slopes and were significantly higher in elevation than Barred Owl sites, whereas unoccupied Spotted Owl sites were not significantly different than Barred Owl sites in slope or elevation.

Our results suggest that Spotted Owls are more likely to abandon a site if Barred Owls take up residence close to that site. Similarly, Kelly et al. (2003) found that occupancy of Spotted Owl sites declined after Barred Owls were detected within 0.8 km, but occupancy was not affected when Barred Owls were located >0.8 km from Spotted Owl site-centers. We suggest that a combination of habitat lost due to timber harvest and the presence of Barred Owls may work synergistically to put Spotted Owl pairs at risk of losing their territories.

Sites in the eastern Washington Cascade Mountains, unoccupied for 4 ($N = 2$), 6 ($N = 3$), and 8 ($N = 1$) yr were reoccupied by Spotted Owls; the marked, replacement Spotted Owls in these cases tended to use the same core areas and, in some sites, even nested in the same nest tree used by previous owls (T. Fleming pers. comm.). Therefore, some of our unoccupied sites may become reoccupied in the future.

Spotted Owl Conservation. Existing metapopulation conservation strategies of the northern Spotted Owl are dependent upon Spotted Owls surviving and reproducing in reserves, and being able to move between reserves via hospitable habitats to facilitate genetic interchange and, if necessary, recolonization (Levins 1968, USDA and USDI 1994a, Caughley and Gunn 1996, Gutiérrez and Harrison 1996, Noon and McKelvey 1996). Our data suggested that Barred Owls caused a reduction in the Spotted Owl population by physically excluding them from historic territories and making those territories unavailable for recolonization, as was suggested by Dunbar et al. (1991), Dark et al. (1998), and Kelly (2001). There is an increasing body of evidence that Barred Owls physically attack Spotted Owls (E. Forsman, J. Mowdy, T. Snetsinger, and G. Stagner pers. comm.), and sometimes may kill them (Leskiw and Gutiérrez 1998). Aside from direct competition for space, it is also likely that Barred and Spotted owls compete for prey (Hamer et al. 2001). In addition, Barred Owls may negatively affect dispersing, juvenile Spotted Owls by creating a hostile environment that inhibits the occupation of vacated Spotted Owl territories and other suitable areas. In our study area, presence of Barred Owls had a greater effect on Spotted Owl site occupancy than did the status of the area as a Spotted Owl reserve. In fact, our data suggest that Barred Owls were more numerous in the reserve areas than Spotted Owls. Continued loss of old-growth and mature forest may reduce the ability of Spotted Owls to persist in the presence of Barred Owls.

We recommend continuing the long-term Spotted Owl demography studies (Franklin et al. 1999)

to track occupancy and reproduction of northern Spotted Owls range-wide. Also, this work should include surveys for Barred Owls to determine if the presence of this species affects Spotted Owl occupancy and reproduction.

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