

BARRED OWL AND SPOTTED OWL POPULATIONS AND HABITAT IN THE CENTRAL CASCADE RANGE OF WASHINGTON

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ABSTRACT.—The Barred Owl (*Strix varia*) has continued to expand its range southward into the northwestern United States from Canada since the 1970s, and has become an established member of the forest avifauna in western Washington. There is increasing concern that it may be competing for resources with the threatened Northern Spotted Owl (*S. occidentalis caurina*) throughout its range. We surveyed for Spotted Owls over an extensive area of the central Cascade Range of Washington during the breeding seasons of 1991–93. Both Spotted Owls and Barred Owls responded to tape recordings and vocal imitations of Spotted Owl calls. By using pair responses or grouping single owl responses from close geographic locations on at least three different survey nights, site centers representing probable breeding pairs or territorial single individuals were designated for both species. A total of 53 Barred Owl and 62 Spotted Owl site centers were identified in the 1280 km² survey area. Barred Owls were found at greatest densities on the wetter, western portions of the Cascade Range. On the driest, eastern portions of this mountain range, Barred Owls were usually found along major river and stream corridors, in the vicinity of forested wetlands, or at higher elevations receiving increased precipitation. We compared the extent of mature, young, and other forest habitats at radii of 0.8 and 1.6 km around site centers of both species. Spotted Owls used sites with greater amounts of mature coniferous forest than did Barred Owls within 0.8 km of site centers across all portions of the study area. Additionally, we found no evidence of mixed-species pairing or hybrids of the two species during the study, suggesting that extensive hybridization may not be occurring where Barred Owls have become firmly established within the range of the Spotted Owl.

KEY WORDS: *Barred Owl*; *Strix varia*; *Northern Spotted Owl*; *Strix occidentalis*; *interbreeding*; *populations*; *habitat*; *Washington*.

Poblaciones y habitat de *Strix varia* y *Strix occidentalis* en el central Cascade de Washington

RESÚMEN.—*Strix varia* ha continuado expandiendo su rango hacia el sur dentro del noroeste de los Estados Unidos desde Canada a partir de 1970. Allí se ha establecido como miembro de la avifauna de bosque en el oeste de Washington. Existe una creciente preocupación de que pueda estar compitiendo por recursos con el amenazado *Strix occidentalis caurina* a lo largo de su rango. Examinamos una vasta area en búsqueda de *Strix occidentalis* en la región del Central Cascade de Washington durante las estaciones reproductivas de 1991–93. Ambos buhos respondieron a las grabaciones e imitación de vocalizaciones de *Strix occidentalis*. Mediante la utilización de respuestas pareadas o la agrupación de respuestas únicas de localidades geográficas cercanas en al menos tres noches diferentes de investigación, fueron encontrados los sitios centrales los cuales probablemente representaron a parejas en reproducción o a individuos territoriales de las dos especies. Un total de 53 sitios centrales de *Strix varia* y 62 sitios centrales de *Strix occidentalis* fueron identificados en los 1280 km² investigados. *Strix varia* fue usualmente encontrado a lo largo de los rios y quebradas, en la vecindad de humedales boscosos o a elevaciones mas altas con mayor precipitación. Comparamos la extensión de bosques maduros y juvenes y otros tipos de habitat boscoso en un radio de 0.8 y 1.6 km alrededor de los sitios de centro de ambas especies. *Strix occidentalis* utilizó sitios con mayor cantidad de bosques de coníferas maduros que *Strix varia* dentro de 0.8 km del sitio de centro a traves de todas las porciones del área de estudio. Adicionalmente, no encontramos evidencia de especies mezcladas en pareja o híbridos de las dos especies durante el estudio sugiriendo que la

hibridación no está ocurriendo en los sitios en los cuales *Strix varia* se ha buen establecido dentro del rango de *Strix occidentalis*.

[Traducción de César Márquez]

The Barred Owl (*Strix varia*) is a relatively recent member of the forest avifauna of Washington state. The species was first reported in the mid-1960s in northeastern Washington. West of there, in the northern Washington Cascades, the first pair was recorded in 1974 (Taylor and Forsman 1976). The Barred Owl began to invade the range of the Northern Spotted Owl (*S. occidentalis caurina*) in southwestern British Columbia by the early 1970s (Dunbar et al. 1991). Barred Owls have apparently become more numerous than Spotted Owls over a short period of time at the northern edge of the Northern Spotted Owl's range. From 1985–88, for example, extensive surveys in southwestern British Columbia found 57 Barred Owl territories and 14 Spotted Owl territories (Dunbar et al. 1991). Similarly, in 1985, Hamer (1988) found 15 Barred Owl territories and 8 Spotted Owl territories in northwestern Washington. By the 1990s, Barred Owls had expanded their range through Oregon and become established in northern California in the southern reaches of the Northern Spotted Owl's range (Dark et al. 1998).

Both Barred Owls and Spotted Owls are similar in size, select mature forest habitats (Gutiérrez et al. 1995, Haney 1997, Mazur et al. 1997), and appear to have some overlap in prey use (Devereaux and Mosher 1984, Gutiérrez et al. 1995). Possible competition between the two species may favor the slightly larger and possibly more aggressive Barred Owl (Sharp 1989, Hamer et al. 1994, Dark et al. 1998). The Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (Thomas et al. 1990) noted that potential competition with the Barred Owl was of immediate concern in maintaining viable Spotted Owl populations in the northern Cascades of Washington (north of Mount Rainier). Considering the rapid spread of this congener across the range of the Northern Spotted Owl, understanding the habitat relationships of the two species in areas where they are now sympatric is important for future conservation planning for this threatened owl.

During extensive surveys for Spotted Owls, we noted that Barred Owls responded regularly to broadcasts of tape recordings and vocal imitations of Spotted Owl calls (see also Dunbar et al. 1991).

We present the results of survey efforts over a 3-yr period, showing relative populations of Barred Owls and Spotted Owls within the area of complete survey coverage. We also investigated whether habitat conditions around territory centers for the two species differed. We hypothesized that mature coniferous forest habitat, known to be important to Spotted Owls, would be used to a greater extent by this species than by Barred Owls.

STUDY AREA AND METHODS

Following listing of the Northern Spotted Owl as a Threatened Species in July 1990, extensive survey programs were initiated to provide site-specific data for the review of timber harvest applications in Spotted Owl habitat. These surveys helped to determine local abundance and distribution of Northern Spotted Owls, particularly in managed forests. We conducted surveys over an extensive and relatively contiguous region of the central Washington Cascades in an area of checkerboard land ownership. The area is typified by alternating sections (1.6 km²) of public and private ownership. Public lands are administered by the U.S. Forest Service (USFS) and, to a lesser extent, by the Washington Department of Natural Resources (DNR). Surveys were inclusive of all ownerships within the survey boundaries.

The area of survey coverage straddled the crest of the Cascade Mountains in central Washington, extending across both the east and west slopes of the range (Fig. 1). This area included major portions of the upper Green and Yakima Rivers and their tributaries, and minor portions of the upper White and Naches River basins. Topography consisted of steep, mountainous terrain deeply bisected by rivers and streams. Elevations ranged from 400–2000 m and weather ranged from rainy, mild winters with cool summers west of the crest to snowy, cold winters with warm summers east of the crest. The study area was predominantly composed of coniferous forest habitats ranging from early to late successional, with a history of timber harvest and fire disturbance on both private and federal lands. Minor portions of the study area were covered by deciduous or mixed forests (primarily in major river valleys), shrub, herb, and grass-dominated habitats, or bare rock and talus.

The rain-shadow effect of the Cascade Range produces a gradient of forest types from west to east, with moist conifer forests occurring west of the crest, and extending east of the crest for variable distances depending on elevation (higher elevations received more precipitation), this type is gradually replaced by dry conifer forests several kilometers east of the crest. We surveyed for owls in nearly all forested habitats up to 1525 m in elevation. Near this elevation, west of the Cascade crest, low-elevation forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) are replaced by stands of Pacific silver fir (*Abies amabilis*), mountain

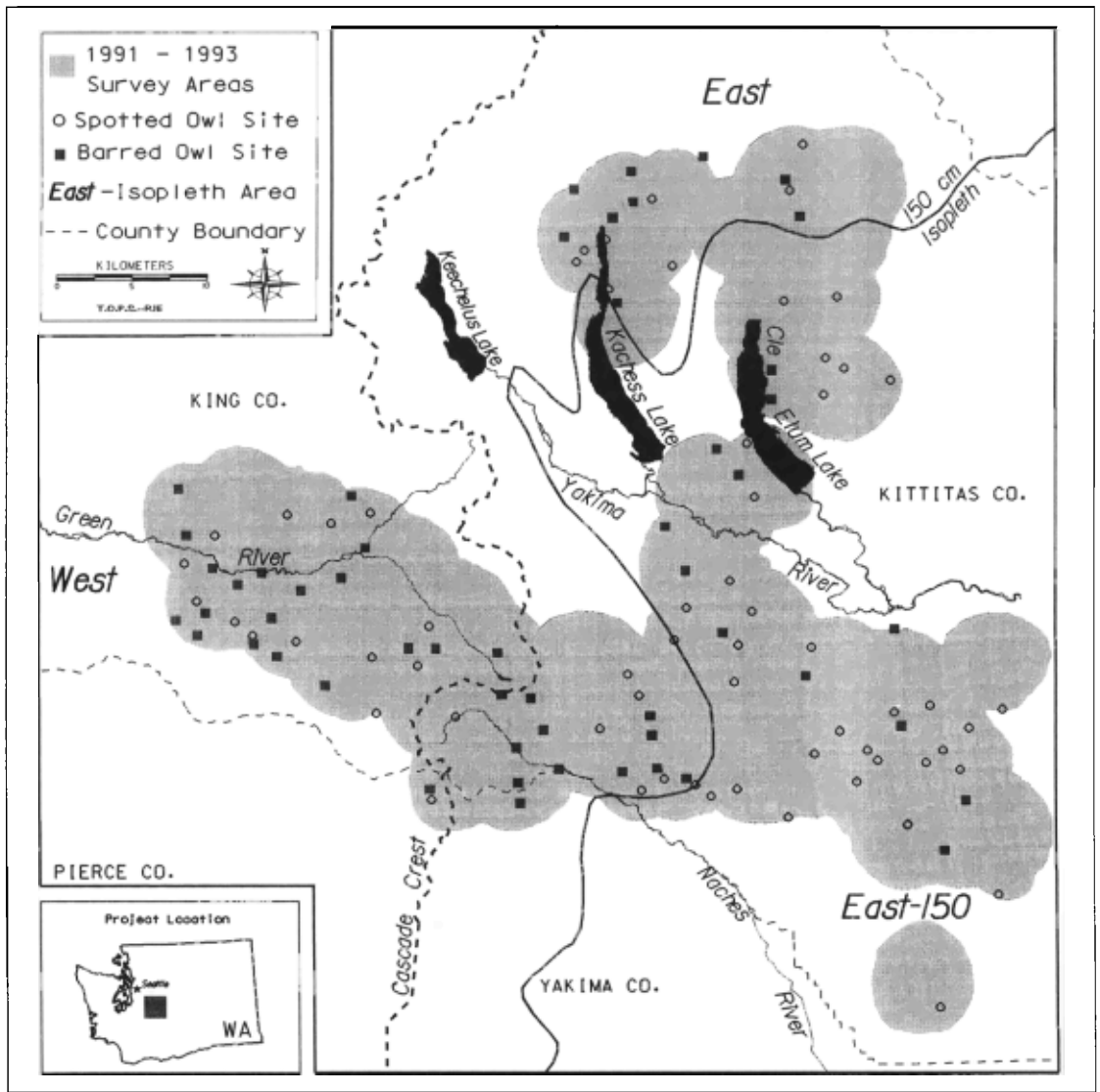


Figure 1. Location of the surveyed area in central Washington showing distribution of Barred Owl and Spotted Owl site centers. The three major subdivisions of the study area based on geography (Cascade crest) and rainfall (150 cm annual isopleth) are also shown.

hemlock (*T. mertensiana*), and noble fir (*A. procera*) at higher elevations. Similarly, low-elevation forests dominated by Douglas-fir, grand fir (*A. grandis*), and Ponderosa pine (*Pinus ponderosa*) in the eastern Cascades are replaced by stands of Pacific silver fir, subalpine fir (*A. lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) at higher elevations. Spotted Owls were not thought to nest above approximately 1525 m in the Washington Cascades (see Allen et al. 1989).

We conducted Spotted Owl surveys from 1991–93, surveying between 15 March–31 August in each year. The

survey season approximated the breeding season for *Strix* owls in the local area. Surveys for Spotted Owls followed U.S. Fish and Wildlife Service (1991, 1992) guidelines for surveying lands proposed for forest management activities. Individual survey areas were established around proposed timber harvest units, extending 2.9 km in radius from the perimeter of each unit (harvest units were 5–35 ha in size). These bounds were selected because a circle of radius 2.9 km (26.4 km²) approximated the average size of a Spotted Owl territory based on regional home range studies (WSFPB 1996). Survey areas often

overlapped, yielding several large regions of complete coverage with rounded perimeters (Fig. 1).

In each survey area, calling stations were established along roads, trails, or on off-trail routes to provide complete audio coverage of all potential habitat of Spotted Owls. Calling stations were typically 0.4–0.8 km apart along roads or trails, with closer spacing in off-trail areas. Surveys consisted of an observer conducting a 10-min visit to each calling station, repeated six times over a survey season, or three times in each of two consecutive survey seasons. All road and most trail stations were visited during hours of darkness, and for safety reasons, some trail and all off-trail stations were visited during the day, usually during afternoon or early evening hours when we suspected owls to be more responsive. During each 10-min calling session, observers imitated calls of Spotted Owls vocally, broadcast a playback of several types of Spotted Owl calls, or used both methods to elicit responses from owls. Calling was interspersed with periods of listening at the observer's discretion, with generally 3–4 min of calls and 6–7 min of listening at each station. Calling was often concentrated at the beginning of the 10-min period, and listening concentrated during the latter half of the 10-min period. Responses from all large owl species were mapped and information on species, sex, movements, and other observations were recorded. All Spotted Owl responses were investigated the following day or as soon as possible to determine reproductive status.

Maps containing Spotted Owl and/or Barred Owl responses from the six survey visits were reviewed following the third and final survey season. Sites where we obtained at least one response from a pair of owls, or at least three responses on three different nights (separated by >7 d) from single owls of either sex within a 0.2-km radius area, were designated as site centers for that species. If an actual nest tree was located, this location then became the site center. The techniques we used to designate site centers for both owl species were essentially identical to procedures used to determine regulatory Spotted Owl site centers by state and federal agencies. Each site center is considered likely to represent a territorial individual or pair (U.S. Fish and Wildlife Service 1992). Previously-known Spotted Owl site centers which were not occupied during our three survey years were not included in the sample. Although we did not follow-up on night responses to determine nest sites for Barred Owls, designation of site centers was usually apparent based on clusters of responses and consistency of response locations in multiple years. We provided six opportunities for territorial owls to respond to our calls and often over three responses were used to determine a site center. In addition, the mountainous terrain helped delimit responses, which were often located in distinct valleys and separated from a nearby site center by an obvious ridge (thereby out of hearing range of the other pair). Simultaneous or near-simultaneous calls from adjacent pairs or singles of the same sex on a given night also helped delimit one site from the next for each species. The actual center was placed on the earliest record of a pair (or nest for Spotted Owls) during a season, and likewise the earliest record of a single if no pair was ever found. Early season responses were assumed to be closer to a potential nest

site than late season responses, although pair responses always took priority over single responses.

We overlaid isopleths of annual precipitation on study area maps to compare the effects of the east-west moisture gradient across the Cascades on owl distribution. We also plotted site centers on habitat maps digitized from 1:64 000 aerial photography. We used mapping that was originally prepared for Spotted Owl management planning based on Washington DNR habitat definitions in use at the time, and separated all habitats into three types: (1) Old Forest Habitat which was dominated by coniferous trees typically over 100 yr old, >60% canopy cover, one to multiple canopy layers, and at least 40% cover of Douglas-fir; (2) Young Forest Habitat which was dominated by trees typically <100 yr old (but of sufficient height and spacing to allow movement of owls during foraging), >60% canopy cover, and typically a single canopy layer; (3) Non-habitat which was made up of forested habitats with overstory trees <10 m in height, stands with <60% canopy cover and/or <40% cover of Douglas-fir, deciduous stands or mixed stands with >25% deciduous overstory, and all forests >1525 m elevation. Shrub, herb and grass-dominated habitats, bare rock and talus slopes, farmland, and water were also included in the Non-habitat category.

To compare habitats near site centers of both species, we drew concentric circles of 0.8- and 1.6-km radius around each site center. Circular areas around Spotted Owl sites have been used in similar investigations of habitat patterns (Lehmkuhl and Raphael 1993, Meyer et al. 1998, Swindle et al. 1999). Habitat comparisons in our study were restricted to mature and young coniferous forest habitats because of the demonstrated importance of mature forests to Spotted Owls (Thomas et al. 1990) and the suggestion that Barred Owls could use stands of younger forest (Hamer 1988).

We followed recent habitat studies of Spotted Owls (Meyer et al. 1998, Swindle et al. 1999) in selecting the two circular areas for determining the nest-site locations of Spotted Owls. Radii of ≤ 0.8 km have been shown to have significant differences in comparisons of habitat around nest sites and random forest sites (Meyer et al. 1998, Swindle et al. 1999), and differences in the amount of old forest may occur up to 1.6 km (Swindle et al. 1999). We stratified owl sites in our area into three subunits based primarily on precipitation criteria: west of the Cascade Range crest, east of the crest to the 150 cm precipitation isopleth, and east of the 150 cm isopleth. Our comparisons of average amounts of each habitat type within the tested radii were achieved using multiple analysis of variance (MANOVA), following tests for normality and use of the Wilks' lambda (likelihood ratio criterion) to test for significant interaction between variables (SYSTAT version 8.0). We randomly sampled circular areas around site centers, and used mutually exclusive (site centers of both species tested at 0.8-km radius were not used for tests at 1.6-km radius), nonoverlapping areas for both radii.

RESULTS

Population Size and Distribution. Spotted Owl surveys, when combined over three breeding sea-

sons, covered 1280 km². Portions of the surveyed area above 1525 m, or extensive areas classified as nonhabitat were not surveyed. We may have missed some Barred Owls by not surveying in forested habitats containing >75% deciduous trees. Large stands of mixed and deciduous forests comprised <2% of the study area and occurred only in the floodplain of the Green and Yakima Rivers. Likewise, stands of <60% canopy closure were uncommon and small in size, and often occurred adjacent to surveyed stands, therefore receiving limited survey coverage (Fig. 1).

A total of 62 Spotted Owl site centers and 53 Barred Owl site centers were identified. Spotted Owls were well-distributed across the area (0.047, 0.043, and 0.053/km² from west to east by subunit; Fig. 1). Barred Owls were most abundant west of the Cascade crest (0.063/km²), with similar densities (0.063/km²) extending east of the crest only within the 150 cm/yr isopleth for annual precipitation. East of this line, Barred Owl densities dropped to 0.019/km². To the west of our survey area within the Cascade Range, only Barred Owls were located during similar surveys from 1991–93 (L. Young pers. comm.). To the east of our study area, several additional Spotted Owl sites and a few Barred Owl sites have been located across northern Kittitas County almost to the forest/sagebrush steppe interface (S. Sovern and M. Taylor pers. comm.). Also, we have found Barred Owls breeding at sites both lower and higher in elevation than known Spotted Owl nest locations. Barred Owls have completely overlapped the known geographic and altitudinal distribution of Spotted Owls in central Washington.

Habitat Analyses. We found no significant differences in the mean amount of all habitat types between Spotted and Barred Owls within the 1.6 km radius analysis area (Wilks' $\lambda = 0.946$, $P = 0.475$) around site centers. Within the 0.8 km radius surrounding Spotted Owl and Barred Owl sites, however, significant differences in mean habitat amounts were detected (Wilks' $\lambda = 0.725$, $P = 0.003$). Spotted Owl sites contained more old forest close to the site center than Barred Owl sites. Within the three geographic regions we tested, MANOVA results indicated that mean amount of habitat differed significantly within the 0.8 km (Wilks' $\lambda = 0.594$, $P = 0.001$) radius. There was consistently more old forest surrounding Spotted Owl sites than Barred Owl sites in all subunits (Table 1). Barred Owl sites also contained more young

forest than Spotted Owl sites in the far west and far east subunits.

In the dry zone of the eastern Cascades east of the 150-cm isopleth, 8 of 12 Barred Owl site centers were found in moister forest situations, such as those along major river or stream drainages or near lakes or wooded swamps or at higher elevations where the true amount of precipitation may actually have exceeded 150 cm/yr. On both slopes of the Cascade Range, several Barred Owl sites occurred in deciduous and mixed forest stands found exclusively in major river valleys. Forest stands dominated by deciduous trees are not considered important Spotted Owl habitat in Washington (WSFPB 1996). East of the 150-cm isopleth, Spotted Owl sites were typically located in coniferous forests on the sides of slopes and were not found in the habitats described above for Barred Owls. West of the 150-cm isopleth and above major river valleys, however, Spotted Owl sites occurred in very similar situations to those of Barred Owls. We did not find Spotted Owl nests in high-elevation, true fir-dominated forests. Our own observations of Barred Owls, plus those of Wright and Hayward (1998), suggest that this species is also more common in lower elevation mixed conifer forests than in high elevation spruce-fir forests.

DISCUSSION

Population Size and Distribution. The full impact of the Barred Owl range expansion into the Pacific Northwest on resident Spotted Owls probably has yet to be fully realized. We detected almost as many Barred Owls as Spotted Owls, and in some portions of the Washington Cascades, Barred Owls have become more numerous than Spotted Owls. We could have missed some territories of both owl species, particularly Barred Owls; however, we received consistent responses from both species at night and during the day, even though we only broadcast Spotted Owl calls. Responses obtained during the day were typically at closer range than at night. Daytime surveys were designed with closer spacing of calling stations and transects to account for this tendency. Even so, we could have missed some owls, particularly Barred Owls, because of individual variation in response levels to calls of a congener.

All Spotted Owl sites known in the survey area were monitored for occupancy and reproduction annually from 1991–98. Of the 62 known sites, 22 were unoccupied at least temporarily by both

Table 1. Comparison of mean hectares of habitat present within selected radii around Barred Owl and Spotted Owl site centers across three geographic regions in the Central Cascade range of Washington.

RADIUS ^b (km)	WEST ^a			EAST ^a			EAST 150 ^a		
	MEAN	95% CI	N	MEAN	95% CI	N	MEAN	95% CI	N
0.8 km									
Old/Mature Forest									
Barred Owl	57	43	10	81	27	11	55	47	4
Spotted Owl	83	32	8	106	42	4	98	30	13
Young Forest									
Barred Owl	72	34	10	42	29	11	41	41	4
Spotted Owl	51	36	8	5	10	4	40	20	13
Non-habitat ^c									
Barred Owl	73	33	10	79	30	11	106	83	4
Spotted Owl	68	35	8	87	33	4	64	20	13
1.6 km									
Old/Mature Forest									
Barred Owl	173	153	8	430	112	9	304	125	8
Spotted Owl	182	136	5	334	85	9	323	97	15
Young Forest									
Barred Owl	354	178	8	91	98	9	163	94	8
Spotted Owl	420	133	5	117	71	9	178	55	15
Non-habitat									
Barred Owl	403	161	8	442	144	9	545	200	8
Spotted Owl	405	42	5	456	156	9	489	103	15

^a West = west of the Cascade Range crest, East = east of the Cascade Range crest but west of the 150 cm/yr rainfall isopleth, East 150 = east of the 150 cm/yr rainfall isopleth.

^b Area within 0.8 km radius = 201 ha; 1.6 km radius = 804 ha.

^c Non-habitat included non-forest, deciduous-dominated forests, and high-elevation forests.

members of the original pairs. Of these 22 sites, half remained unoccupied through 1998. Of the remaining 11 sites, six were reoccupied by different Spotted Owl pairs or single individuals, while Barred Owls were present at or near five site centers. In most cases, Barred Owls were already present in the vicinity (≤ 0.8 km) prior to the disappearance of the Spotted Owl pairs. In one instance, a newly established pair of Spotted Owls nested within 1 km (and hearing distance) of an established Barred Owl site. Surveys over additional years are needed to determine whether Spotted Owls regularly reoccupy sites in close proximity to Barred Owl territories.

Habitat Analyses. In portions of the western Washington Cascades west of our study area where less old forest remained, Barred Owls have occupied second-growth Douglas-fir/western hemlock stands with remnant large trees and snags which provide nest cavities. Spotted owls have been known to occur in landscapes where young forests predominate (Forsman et al. 1988, Irwin et al.

1991), but they persist at low densities and typically nest in a patch of old forest. In our study area, where relatively large stands (>200 ha) of old forest habitat remained, surrounded by a mosaic of managed and unmanaged fire-regenerated habitat, both Spotted Owls and Barred Owls occupied nesting territories and produced young. Our data suggested that Barred Owls persisted in areas with less old forest than Spotted Owls.

Within conservation areas designed for Spotted Owl habitat protection, management options that consolidate and protect preferred habitat for Spotted Owls in well-spaced, large blocks (>100 ha) may help them compete with Barred Owls in Cascade Range forests. Recent studies by Meyer et al. (1998) and Swindle et al. (1999) have also noted a preference for an unfragmented patch of old forest around Spotted Owl nest sites. This does not mean that Barred Owls cannot successfully occupy areas of extensive cover of old forest. Observations by Wright and Hayward (1998) and our own observations in neighboring wilderness areas and na-

tional parks indicated that territorial Barred Owls can occur in wilderness valleys with extensive cover of old forest.

Some competition for resources likely takes place where the two species are sympatric because of significant overlap in habitat use, prey species, and nest-site preferences. Spotted Owls and Barred Owls were previously sympatric in only one other area in North America, at the southern limit of the ranges of both species in the southern Sierra Madre Occidental of Mexico (Enríquez-Rocha et al. 1993, Howell and Webb 1995). In Mexico, there are two different subspecies and the duration of the sympatry has been longer. In our study area, the northern subspecies of both owls appear to co-exist in very similar habitats in the wet, western Cascades, but they may be exhibiting greater habitat separation in the eastern Cascades. In these dryer forests, the predominance of Spotted Owls in conifer forests at mid-slope (Buchanan et al. 1995), and Barred Owls in forested wetlands, mixed riparian stands, and high elevation moist coniferous forests, mirrored the habitat use of the species over the majority of their respective ranges. Spotted Owls, outside the coastal Pacific Northwest, are primarily found in relatively-dry, western mountains, while Barred Owls occur in more mesic habitats in eastern mixed or deciduous forests and boreal forests.

Barred Owls were already well-established on our study area by the time we began our surveys. We found no mixed-species (Barred Owl/Spotted Owl) pairs or hybrid owls, but hybrids have been reported from Washington and other parts of the Northern Spotted Owl range (Hamer et al. 1994). Widespread hybridization in the central Washington Cascades did not appear to be continuing. As shown in other species (Short 1969, Rohwer 1972), it is likely that once Barred Owls established self-sustaining local populations, individuals of the invading species no longer had trouble finding conspecific mates, minimizing the incidence of mixed-species pairing.

Although this study suggests only minor differences in the amount of old and mature forest habitat surrounding Spotted and Barred Owl site centers based on the broad seral stages used in our analyses, perhaps more detailed habitat use studies would indicate more partitioning. The extent that habitat or niche separation will keep the two species from competing directly for resources should be considered speculative. However, direct com-

petition in some habitats appears likely and may negatively affect Spotted Owl population recovery.

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LITERATURE CITED

- ALLEN, H.L., K.R. DIXON, AND K.L. KNUTSON. 1989. Cooperative administrative study to monitor Spotted Owl management areas in national forests in Washington Unpubl. Rep., Washington Depart. Wildl., Olympia WA, U.S.A.
- BUCHANAN, J.B., L.L. IRWIN, AND E.L. MCCUTCHEN. 1995. Within-stand nest site selection by Spotted Owls in the eastern Washington Cascades. *J. Wildl. Manage.* 59: 301–310.
- DARK, S.J., R.J. GUTIÉRREZ, AND G.I. GOULD, JR. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* 115:50–56.
- DEVEREAUX, J.G. AND J.A. MOSHER. 1984. Breeding ecology of the Barred Owl in the central Appalachians *Raptor Res.* 18:39–58.
- DUNBAR, D.L., B.P. BOOTH, E.D. FORSMAN, A.E. HETHERINGTON, AND D.J. WILSON. 1991. Status of the Spotted Owl, *Strix occidentalis*, and Barred Owl, *Strix varia*, in southwestern British Columbia. *Can. Field-Nat.* 105 464–468.
- ENRÍQUEZ-ROCHA, P., J.L. RANGEL-SALAZAR, AND D.W. HOLT. 1993. Presence and distribution of Mexican owls: a review. *J. Raptor Res.* 27:154–160.
- FORSMAN, E.D. 1988. A survey of Spotted Owls in young forests in the northern Coast Range of Oregon. *Murrelet* 69:65–68.
- GUTIÉRREZ, R.J., A.B. FRANKLIN, AND W.S. LAHAYE. 1995. Spotted Owl (*Strix occidentalis*). Pages 1–28 in A. Poole and F. Gill [Eds.], *The birds of North America*, No. 179. The Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, DC U.S.A.
- HAMER, T.E. 1988. Home range size of the Northern Barred Owl and Northern Spotted Owl in western Washington. M.S. thesis, W. Wash. Univ., Bellingham, WA U.S.A.

- , E.D. FORSMAN, A.D. FUCHS, AND M.L. WALTERS. 1994. Hybridization between Barred and Spotted Owls. *Auk* 111:487–492.
- HANEY, J.C. 1997. Spatial incidence of Barred Owl (*Strix varia*) reproduction in old-growth forest of the Appalachian Plateau. *J. Raptor Res.* 31:241–252.
- HOWELL, S.N.G. AND S.B. WEBB. 1995. The birds of Mexico and northern Central America. Oxford Univ. Press, New York, NY U.S.A.
- IRWIN, L., T.L. FLEMING, S.M. SPEICH, AND J.B. BUCHANAN. 1991. Spotted Owl presence in managed forests of southwestern Washington. Tech. Bull. No. 601. National Council of the Paper Industry for Air and Stream Improvement, Inc., Corvallis, OR U.S.A.
- LEHMKUHL, J.F. AND M.G. RAPHAEL. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.* 57:302–315.
- MAZUR, K.M., P.C. JAMES, M.J. FITZSIMMONS, G. LANGEN, AND R.H.M. ESPIE. 1997. Habitat associations of the Barred Owl in the boreal forest of Saskatchewan, Canada. *J. Raptor Res.* 31:253–259.
- MEYER, J.S., L.L. IRWIN, AND M.S. BOYCE. 1998. Influence of habitat abundance and fragmentation on Northern Spotted Owls in western Oregon. *Wildl. Monogr.* 139: 1–51.
- ROHWER, S.A. 1972. A multivariate assessment of interbreeding between the meadowlarks, *Sturnella*. *Syst. Zool.* 21:313–338.
- SHARP, D.U. 1989. Range extension of the Barred Owl in western Washington and first breeding record on the Olympic Peninsula. *J. Raptor Res.* 23:179–180.
- SHORT, L.L. 1969. Taxonomic aspects of avian hybridization. *Auk* 86:84–105.
- SWINDLE, K.A., W. J. RIPPLE, E.C. MESLOW, AND D. SCHAFER. 1999. Old-forest distribution around Spotted Owl nests in the central Cascade Mountains, Oregon. *J. Wildl. Manage.* 63:1212–1221.
- TAYLOR, A.L., JR. AND E.D. FORSMAN. 1976. Recent range extensions of the Barred Owl in western North America, including the first records for Oregon. *Condor* 78: 560–561.
- THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON, AND J. VERNER. 1990. A conservation strategy for the Northern Spotted Owl. U.S. Fish Wildl. Serv. Portland, OR U.S.A.
- U.S. FISH AND WILDLIFE SERVICE. 1991. Protocol for surveying proposed management activities that may impact Northern Spotted Owls. U.S. Fish Wildl. Serv., Portland, OR U.S.A.
- . 1992. Protocol for surveying proposed management activities that may impact Northern Spotted Owls (Revised). U.S. Fish Wildl. Serv., Portland, OR U.S.A.
- WASHINGTON STATE FOREST PRACTICES BOARD (WSFPB). 1996. Final environmental impact statement on forest practices rule proposals for: Northern Spotted Owl, Marbled Murrelet, Western Gray Squirrel. Wash. Dept. Nat. Resources, Olympia, WA U.S.A.
- WRIGHT, A.L. AND G.D. HAYWARD. 1998. Barred Owl range expansion into the central Idaho wilderness. *J. Raptor Res.* 32:77–81.

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