

FOREST STRUCTURE WITHIN BARRED OWL (*STRIX VARIA*) HOME RANGES IN THE EASTERN CASCADE RANGE, WASHINGTON

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ABSTRACT.—Competitive interactions with Barred Owls (*Strix varia*) are an important factor contributing to the decline of the Northern Spotted Owl (*Strix occidentalis caurina*) population. Understanding the degree of similarity in fine-scale habitat associations for Spotted Owls and Barred Owls will help land managers evaluate whether there are specific vegetation conditions that could favor Spotted Owls over Barred Owls. From March 2004 to September 2006, I tracked 14 radio-tagged Barred Owls in the Okanogan-Wenatchee National Forest in the eastern Cascade Range, Washington. I analyzed forest structure characteristics from 170 plots sampled within areas used by the radio-tagged owls. I identified three forest types present within the Barred Owl home ranges, including: (1) open ponderosa pine (*Pinus ponderosa*), (2) simple-structure Douglas-fir (*Pseudotsuga menziesii*), and (3) complex-structure grand fir (*Abies grandis*). I compared individual forest structure characteristics and the three forest types to the intensity of Barred Owl use based on repeated measures of seasonal utilization distribution values at each plot using hierarchical mixed-effects models. Intensity of Barred Owl use during the breeding season was higher in areas with greater abundance of grand fir trees, taller and more diverse tree heights, more total trees per ha, more trees 12.7–22.9 cm dbh, more tree canopy >4.9 m, and less ground-cover vegetation <0.6 m. During the nonbreeding season, intensity of Barred Owl use was higher in areas with more trees 12.7–22.9 cm dbh, more total trees per ha, gentle slopes, and increased tree species diversity. Barred Owls used the structurally diverse grand fir forest type more intensively than the other two types during the breeding season. Intensity of use did not differ across the types during the nonbreeding season. Forest structure characteristics used by Barred Owls in this study were within the range of conditions reported to be used by Spotted Owls in the eastern Cascade Range.

KEY WORDS: Northern Spotted Owl; *Strix occidentalis caurina*; Barred Owl; *Strix varia*; forest management; habitat use; niche partitioning; telemetry.

ESTRUCTURA DEL BOSQUE DENTRO DEL ÁREA DE CAMPEO DE *STRIX VARIA* EN LA CORDILLERA CASCADE ORIENTAL, WASHINGTON

RESUMEN.—Las interacciones competitivas con *Strix varia* son un factor importante que contribuye a la disminución de la población de *Strix occidentalis caurina*. Es de vital importancia entender el grado de similitud en las asociaciones de hábitat a pequeña escala de *S. o. caurina* y *S. varia* para ayudar a los gestores del territorio a evaluar si existen condiciones de vegetación específicas que pudieran favorecer a *S. o. caurina* sobre *S. varia*. Entre marzo de 2004 y septiembre de 2006, pude seguir mediante radio-seguimiento convencional 14 individuos de *S. varia* en el Parque Nacional Okanogan-Wenatchee en la Cordillera Cascade Oriental, Washington. Analicé características de la estructura del bosque en 170 parcelas distribuidas dentro de las áreas utilizadas por los búhos equipados con radioemisores. Identifiqué tres tipos de bosques presentes dentro del área de campeo de *S. varia*: (1) bosque de *Pinus ponderosa* abierto, (2) bosque de *Pseudotsuga menziesii* de estructura simple y (3) bosque de *Abies grandis* de estructura compleja. Comparé las características individuales de la estructura del bosque y los tres tipos de bosques con la frecuencia de uso por parte de *S. varia*, basado en mediciones repetidas de los valores de distribución del uso estacional de cada parcela, empleando modelos jerárquicos de efectos mixtos. La frecuencia de uso de *S. varia* durante la época reproductiva fue mayor en las áreas con mayor abundancia de *A. grandis*, de árboles más altos y de alturas más diversas, con mayor número total de árboles por hectárea, mayor número de árboles con diámetros a la altura del pecho (dap) entre 12.7 y 22.9 cm, dosel con una altura >4.9 m y vegetación de sotobosque menor a <0.6 m. Durante la época no reproductiva, la frecuencia de uso de *S. varia* fue mayor en las áreas con mayor número de árboles con dap entre 12.7–22.9 cm, mayor número total

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de árboles por hectárea, pendientes poco pronunciadas y mayor diversidad de especies arbóreas. Durante la época reproductiva, *S. varia* utilizó con mayor intensidad los bosques estructuralmente diversos de *A. grandis* que los otros dos tipos de bosque. La frecuencia de uso no difirió entre los tipos de bosque durante la época no reproductiva. Las características de la estructura del bosque que usó *S. varia* en este estudio se encuentran dentro del rango de las condiciones requeridas por *S. o. caurina* en la Cordillera Cascade Oriental.

[Traducción del equipo editorial]

Interaction with Barred Owls (*Strix varia*) is an important factor associated with Northern Spotted Owl (*Strix occidentalis caurina*) population declines (Olson et al. 2005, Dugger et al. 2011, Forsman et al. 2011, U.S.F.W.S. 2011). Spotted Owl populations in Washington and northern Oregon declined by approximately 40–60% from 1989 to 2008 (Forsman et al. 2011). Understanding the degree of similarity in fine-scale habitat associations for Spotted Owls and Barred Owls will help land managers evaluate whether there are specific vegetation conditions that could favor Spotted Owls over Barred Owls.

Many studies have described landscape and fine-scale habitat associations for Spotted Owls (reviewed by Courtney et al. 2004, U.S.F.W.S. 2011), but less information is available for Barred Owls (reviewed by Livezey 2007). Several studies have presented general information on Barred Owl habitat associations from photo-interpreted or GIS maps (Herter and Hicks 2000, Pearson and Livezey 2003, Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014), and one presented field measurements of vegetation characteristics at Barred Owl nests (Buchanan et al. 2004), but to my knowledge none has reported fine-scale field measurements of forest structure characteristics within Barred Owl home ranges. Using data from the radiotelemetry study presented here, Singleton et al. (2010) reported that Barred Owls tended to locate their home ranges on gentle slopes in relatively low topographic settings, in areas with more green vegetation, more overstory tree canopy cover, and larger trees than the surrounding landscape, but they did not detect substantial within-home-range habitat selection patterns based on GIS vegetation maps derived from remotely sensed imagery.

The goal of this study was to relate intensity of space use by Barred Owls within their home ranges to stand-level forest structure characteristics. I had two objectives in this study: (1) to identify forest structure characteristics that are associated with Barred Owl use, and (2) to quantify the suite of forest structure characteristics found within Barred Owl home ranges and evaluate how typical combi-

nations of those characteristics relate to intensity of Barred Owl use.

STUDY AREA

My study area encompassed 309 km² in the interior mixed-conifer vegetation zone near Leavenworth and Lake Wenatchee in Chelan County, Washington (120°35'W, 47°48'N; Fig. 1). This area was within the Wenatchee River Ranger District of the Okanogan-Wenatchee National Forest. Vegetation conditions in the study area were influenced by the strong moisture gradients associated with the rain-shadow effect of the Cascade Mountains and local topography. Average annual precipitation across the study area ranged from 150 cm in the northwest to 50 cm in the southeast. Forests in the northwestern portion of the study area (closest to the Cascade crest) were predominantly in moist grand fir (*Abies grandis*) series plant associations, with Douglas-fir (*Pseudotsuga menziesii*) and grand fir as common overstory species (Lillybridge et al. 1995). The southeastern portion of the study area (farthest from the Cascade crest) supported dry grand fir and Douglas-fir series plant associations, with northern exposures often having an overstory of Douglas-fir, and southern exposures characterized by open ponderosa pine (*Pinus ponderosa*) or non-forest (Lillybridge et al. 1995).

METHODS

Quantifying Barred Owl Habitat Use. I quantified intensity of Barred Owl habitat use based on seasonal utilization distributions. From March 2004 to September 2006, field personnel tracked 14 radio-tagged Barred Owls, including at least one individual from 12 different resident pairs (Singleton et al. 2010). Locations of tagged owls were documented at least twice a week, with a minimum of 24 hr between locations. Locations documented during the breeding season (1 March to 30 September) were distributed among midday (0800–1600 H; 37% of locations), morning and evening (0400–0800 H and 1500–2000 H; 35%), and night (2000–0400 H; 29%). During the nonbreeding season (1 October

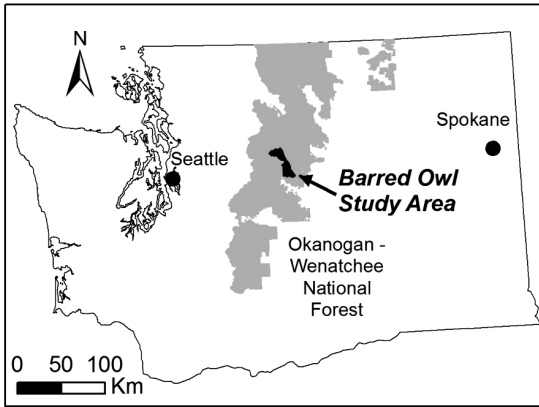


Figure 1. Location of the Barred Owl radiotelemetry study area in the eastern Cascade Range, Washington.

to 28 February), locations were generally collected during midday (87% of locations) because of safety considerations associated with over-snow travel required to access the sites. I calculated utilization distributions for each year and season during which an owl had ≥ 30 radiotelemetry locations (Singleton et al. 2010). A utilization distribution is a probability density function that estimates the probability of finding the tagged animal at any given point within the home range based on the observed spatial distribution of recorded locations (Marzluff et al. 2004, Millsaugh et al. 2006; Fig. 2). Lower utilization distribution values indicate more intense use. I derived the utilization distributions from fixed-kernel seasonal home ranges mapped at 5% increments using the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997). I used a fixed kernel density smoothing factor (h) of 150 m for all kernel home ranges based on the approximate mean of least-squares cross validation calculations for each seasonal home range. Using a single value for h ensured that the level of kernel smoothing was consistent across all of the seasonal utilization distributions. I determined the outer boundary (the 100% isopleth) of the utilization distribution for each seasonal home range based on a 150-m buffer of the minimum convex polygon derived from the radiotelemetry locations for that season. These utilization distributions provided repeated measures of the intensity of use for each season an individual Barred Owl was radio-tagged (Singleton et al. 2010).

Forest Structure Measurements. Field personnel measured forest structure characteristics at plots that were randomly located within Barred Owl

home ranges. Sample plots were located ≥ 30 m from any stand edge to ensure uniform vegetation conditions within the plot, and only one plot was located within a randomly selected stand. Stands were delineated based on the Wenatchee River Ranger District GIS vegetation map updated using orthophoto and remote sensing information (Okanogan-Wenatchee National Forest, Wenatchee, Washington, U.S.A.; corporate GIS data). The goal was to sample approximately 15 plots at each pair site and 10 plots within each utilization distribution. Preliminary analysis of the sample plot data collected during 2006 indicated that areas with higher levels of Barred Owl use were inadequately represented in the random sample. In 2008, 15 additional plots in randomly selected stands that had been heavily used by Barred Owls were sampled.

At each sample plot, field personnel measured live and dead trees, logs, forest canopy characteristics, and other stand structure information (Table 1). Measurements for all trees >12.7 cm dbh within a 7.3-m-radius (0.02 ha) plot, and all trees >23 cm dbh within an 18-m-radius (0.10 ha) plot were recorded. Diameter at midpoint (dmp) and length for all logs >12.7 cm dmp encountered along a 22-m transect following a random azimuth with the midpoint at the plot center were also recorded. In addition, field personnel calculated percent cover for four vegetation layers (<0.6 m, 0.6–1.8 m, 1.8–4.9 m, and >4.9 m) using a moosehorn densitometer to determine presence or absence of foliage within each layer at 1-m intervals along the 22-m transect, and calculated the proportion of those points with foliage present to derive percent cover for each layer. Stand structure measurement procedures followed U.S.D.A. Forest Service Forest Inventory and Analysis (FIA) protocols (U.S.F.S. 2005). All height measurements were recorded with laser hypsometers (Opti-Logic Corp., Tullahoma, Tennessee, U.S.A.; model 100LH). These data were collected from August to October 2006 and in August 2008. All covariates were measured in the field except solar radiation, which was estimated using the ArcGIS solar analyst tool (version 9.3, Environmental Sciences Research Institute, Redlands, California, U.S.A.).

Identifying Forest Types. I used hierarchical clustering to identify a limited number of forest types that represented common combinations of forest structure attributes. To conduct the cluster analysis, I standardized the covariate values by subtracting the mean and dividing by the standard deviation

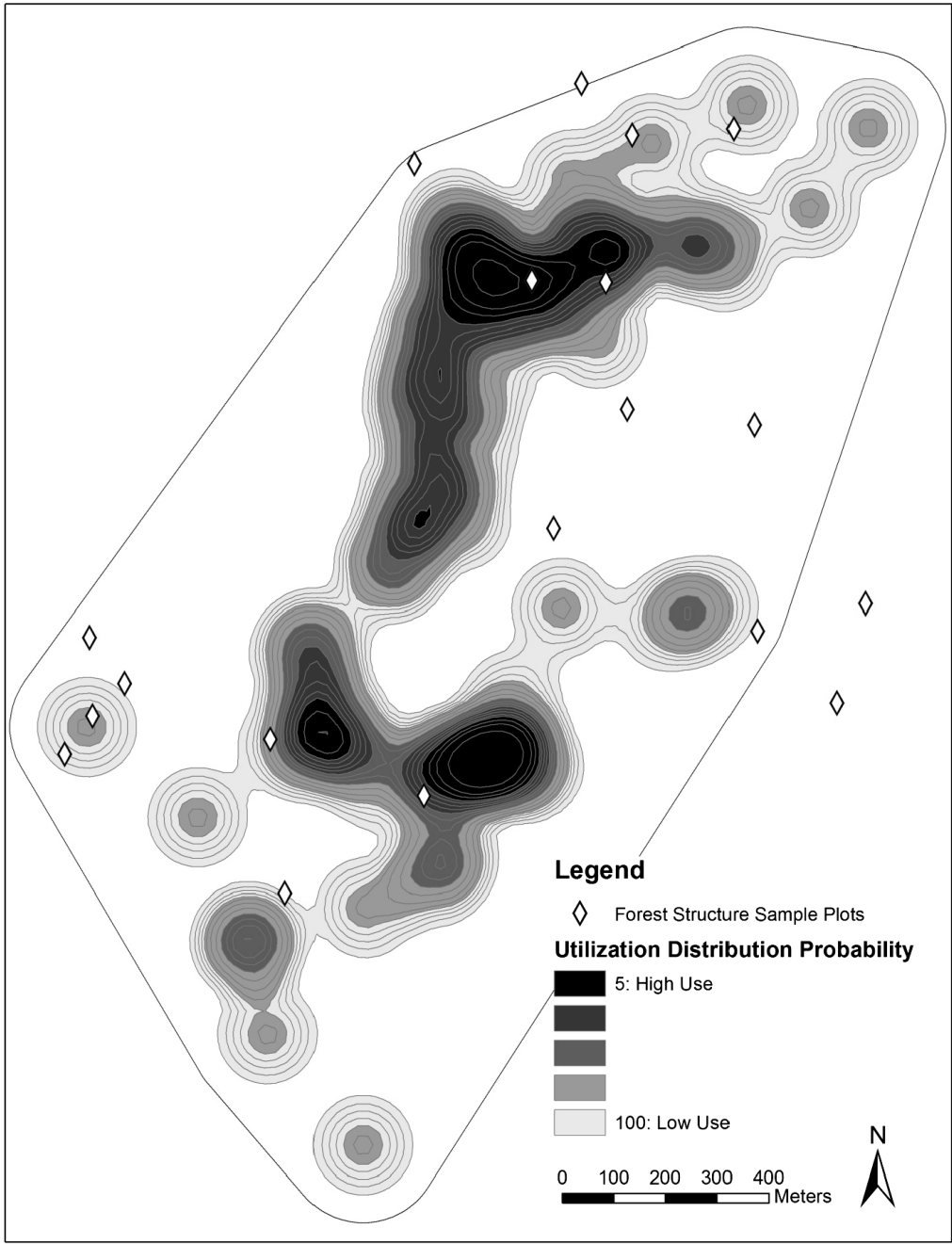


Figure 2. An example utilization distribution map for a male Barred Owl in the eastern Cascade Range, Washington, during the 2006 breeding season, showing utilization distribution probability isopleths (i.e., intensity of use within the home range) and forest structure sample plot locations. Darker areas had higher intensity of use.

Table 1. Forest structure variable names, descriptions, units of measurement, mean values, and standard deviations for attributes measured at 170 plots within Barred Owl home ranges in the eastern Cascade Range, Washington. These values were used to standardize covariates for hierarchical cluster and mixed-effects model analysis.

VARIABLE NAME	DESCRIPTION	UNITS	MEAN	SD
COVER1	Layer 1 vegetation cover, <0.6 m height	percent	54.74	25.66
COVER2	Layer 2 vegetation cover, 0.6–1.8 m height	percent	40.89	23.87
COVER3	Layer 3 vegetation cover, 1.8–4.9 m height	percent	35.77	20.40
COVER4	Layer 4 vegetation cover, >4.9 m height	percent	47.26	22.22
LOGS	Count of logs >22.9 cm diameter at midpoint encountered along a 22 m transect	count	0.54	0.99
MTOE_PR	Proportion of trees infected with mistletoe	proportion	0.08	0.16
PR_ABGR	Proportion of dominant and subdominant trees that are grand fir	proportion	0.16	0.23
PR_PIPO	Proportion of dominant and subdominant trees that are ponderosa pine	proportion	0.22	0.29
PR_PSME	Proportion of dominant and subdominant trees that are Douglas-fir	proportion	0.49	0.35
SLOPE	Slope	degrees	15.21	10.87
SN_HA	Snags >22.9 cm dbh per ha	count	14.45	21.24
SOLR	Solar energy (annual daily mean hundreds of watt-hr/m ²)	Watt-hr/m ²	20.88	4.24
SW_DIV	Shannon–Weiner tree diversity	index	0.67	0.42
TH_S2	Trees per ha, size class 2 (12.7–22.9 cm dbh)	count	27.22	28.51
TH_S3	Trees per ha, size class 3 (23.0–50.8 cm dbh)	count	66.68	44.58
TH_S4	Trees per ha, size class 4 (50.9–101.6 cm dbh)	count	38.37	37.33
TH_S5	Trees per ha, size class 5 (>101.6 cm dbh)	count	1.50	7.25
TH_TOT	Total trees per ha >12.7 cm dbh	count	133.77	65.81
TR_HT_MN ^a	Mean tree height	m	23.42	7.98
TR_HT_SD ^b	Standard deviation of tree height	m	6.46	3.54
TR_ULC_MN ^a	Mean height to unconsolidated live tree crown	m	10.20	4.42
TR_ULC_SD ^b	Standard deviation of height to unconsolidated live tree crown	m	4.46	4.63

^a Mean tree height or height to live crown for dominant and subdominant trees within each plot. Mean and SD indicate the mean and SD of mean tree heights across plots.

^b Standard deviation of tree height or height to live crown for dominant and subdominant trees within each plot. Mean and SD indicate the mean and SD of the SD of tree heights across plots.

using the *scale* function in R (version 15.0, R Development Core Team, Vienna, Austria). I generated a distance matrix using Euclidean distance (with the *vegdist* function in the *vegan* package in R). I used hierarchical cluster analysis to classify plots with similar forest structure characteristics into forest type groups (using the *hclust* function with the Ward method, in the *stats* package in R).

Mixed-effects Model Analysis. I assessed the relationship between individual forest structure characteristics or forest type and intensity of Barred Owl use at each sample plot using hierarchical mixed-effects linear models. The response variable was the intensity of Barred Owl use as represented by repeated measures of seasonal utilization distribution probability values at the sample plot centroids. The predictor variable for each model was the standard-

ized value of each forest structure characteristic recorded at the sample plots (Table 1), or forest type at each plot. I evaluated the forest type models using a no-intercept form to calculate use intensity estimates and 95% confidence intervals of those estimates for each forest type (Faraway 2005). I analyzed breeding season (1 March to 30 September) and nonbreeding season (1 October to 28 February) use separately. I expected that closed-canopy forest stands with more complex stand structure, including large trees, logs, and snags, would be used more intensively by resident Barred Owls than open stands or stands without those structural elements.

Hierarchical mixed-effects models provide a framework for analyzing nonindependent repeated measures data with different sampling intensity across hierarchically correlated study units, like

Table 2. Number of forest structure sampling plots within each seasonal utilization distribution for Barred Owls monitored during three breeding seasons and two nonbreeding seasons in the eastern Cascade Range, Washington. Cells with dashes (-) indicate that a utilization distribution for that individual was not calculated for that season.

OWL	BREEDING SEASON			NONBREEDING SEASON	
	2004	2005	2006	2004	2005
ACF	-	9	9	-	13
BMF	-	39	12	-	44
CBF	9	-	-	9	-
CBM	5	12	11	13	20
CRF	-	-	-	11	-
CRM	12	17	16	19	19
DCF	-	9	-	-	8
ECM	-	27	-	-	-
EEM	-	12	-	-	-
FLM	10	9	-	12	-
GAF	-	10	-	-	-
GCM	-	4	1	-	5
MCM	-	4	10	-	8

the seasonal Barred Owl utilization distributions analyzed in this study (Zuur et al. 2009). I specified three random effects levels for the mixed-effects models to address hierarchical correlation patterns within my data. The random effects levels were: (1) the owl pair, to account for correlation between overlapping utilization distributions for paired birds, (2) the individual bird, to account for correlation when more than one breeding or nonbreeding season utilization distribution was recorded for an individual, and (3) a unique code for each seasonal utilization distribution to correctly address the unbalanced sampling across utilization distributions and the repeated measures of use at sample plots that fell within more than one seasonal utilization distribution (Zuur et al. 2009). I conducted the hierarchical mixed-effects modeling analysis using the *lmer* function in the *nlme* package in R. Previous analysis of this data set included model selection and model averaging analysis using an information theoretic approach (Singleton 2013). I have chosen not to include that analysis here because it did not provide substantial ecological insights beyond the analysis presented here, and the comparison of intensity of use across the forest types provided a more accessible description of the typical combinations of forest characteristics found in stands within Barred Owl home ranges.

RESULTS

I compared forest structure characteristics at 170 sample plots to repeated measures of use by 13 Barred Owls, based on a total of 21 breeding season and 12 nonbreeding season utilization distributions (Table 2). Use intensity from more than one seasonal utilization distribution was assessed for most of the sample plots, resulting in 247 total measures of use intensity during the breeding season and 181 measures of use during the nonbreeding season. Tracking duration varied for individual owls because of issues associated with transmitter retention and recapture of previously tagged owls. Two Barred Owls were equipped with radio transmitters throughout the study and had sufficient location data to calculate utilization distributions for all seasons; the other owls were radio-tagged for shorter intervals (Table 2). One owl was captured and radio-tagged, but did not retain the transmitter long enough to provide an adequate number of locations for calculating a utilization distribution. The number of forest structure plots sampled within each seasonal utilization distribution ranged from one to 44 (mean 13.0; Table 2). Seasonal radiotelemetry results and home-range sizes for these Barred Owls were reported by Singleton et al. (2010).

The mixed-effects models for the individual forest structure characteristics indicated that Barred Owl intensity of use during the breeding season increased with abundance of grand fir, variation in tree height, trees per ha of any size, canopy closure >4.9 m, trees 12.7–22.9 cm dbh, tall trees, and open ground cover <0.6 m (coefficient estimate $P < 0.05$, Table 3). During the nonbreeding season, Barred Owl intensity of use increased with abundance of trees 12.7–22.9 cm dbh, gentle slopes, tree species diversity, and trees per ha of any size (coefficient estimate $P < 0.05$, Table 3).

The hierarchical cluster analysis identified three forest structure types that captured most of the variation across the sampling plots (Fig. 3). Type 1 stands were predominantly recently disturbed or open ponderosa pine stands that had fewer large trees, more cover of low vegetation (<0.6 m), less upper-layer canopy cover >4.9 m, and fewer logs and snags than the other types (Table 4). Type 2 stands were Douglas-fir dominated stands that had intermediate amounts of upper-layer canopy cover >4.9 m, ground cover <0.6 m, and intermediate structural diversity (including snags, logs, and trees >50 cm dbh) relative to the other two types (Table 4). Type 3 stands had a mix of grand fir and Douglas-fir trees, had less ground cover <0.6 m,

Table 3. Mixed-effects model results relating individual forest structure variables to intensity of Barred Owl use during the breeding season ($df = 225$) and nonbreeding season ($df = 168$) in the eastern Cascade Range, Washington. Estimates of fixed-effects shown are the intercept, coefficient (β), standard error of the coefficient (SE), and probability that the coefficient is equal to zero (P). The response variable is the utilization distribution probability, for which low values indicate high use. Negative β coefficients indicate more intensive use as covariate values increase. Attribute values were standardized by subtracting the mean and dividing by the standard deviation for the mixed-effects model analysis. Bold font indicates models with $P < 0.05$.

VARIABLE	BREEDING SEASON				NONBREEDING SEASON			
	INTERCEPT	β	SE	P	INTERCEPT	β	SE	P
COVER1	73.27	0.15	0.07	0.03	80.11	0.12	0.06	0.06
COVER2	86.31	-0.12	0.07	0.10	89.19	-0.06	0.07	0.37
COVER3	86.91	-0.15	0.09	0.07	90.63	-0.11	0.08	0.16
COVER4	91.30	-0.21	0.08	0.01	90.27	-0.07	0.07	0.34
LOGS	82.44	-1.83	1.54	0.23	86.38	0.36	1.26	0.77
MTOE_PR	80.60	9.18	10.90	0.40	85.54	10.18	9.84	0.30
PR_ABGR	86.70	-34.17	7.50	0.00	88.63	-10.75	7.54	0.16
PR_PIPO	78.26	12.26	6.89	0.08	84.99	1.05	6.23	0.87
PR_PSME	79.00	6.33	5.44	0.25	86.51	3.64	5.10	0.48
SLOPE	80.48	0.07	0.16	0.69	81.23	0.44	0.15	0.00
SN_HA	83.70	-0.16	0.09	0.06	89.00	-0.14	0.08	0.07
SOLR	82.64	-0.06	0.46	0.90	97.59	-0.50	0.48	0.30
SW_DIV	85.95	-6.98	4.45	0.12	94.90	-11.08	3.90	0.01
TH_S2	85.52	-0.15	0.06	0.02	92.33	-0.21	0.05	0.00
TH_S3	86.28	-0.07	0.04	0.08	89.30	-0.04	0.04	0.36
TH_S4	83.19	-0.05	0.05	0.30	85.91	0.02	0.04	0.68
TH_S5	81.01	0.19	0.22	0.39	87.10	-0.22	0.23	0.34
TR_HT_MN	94.72	-0.58	0.24	0.02	85.32	0.06	0.21	0.79
TR_HT_SD	93.43	-1.89	0.53	0.00	87.60	-0.15	0.51	0.77
TR_TOT	92.92	-0.09	0.03	0.00	94.64	-0.05	0.03	0.03
TR_ULC_MN	83.00	-0.16	0.41	0.71	89.68	-0.28	0.36	0.45
TR_ULC_SD	82.47	-0.24	0.29	0.42	85.72	0.21	0.28	0.46

had more upper-level canopy cover (>4.9 m), and much greater overall structural diversity, including more snags, logs, and large trees >50 cm dbh than the other types (Table 4). I refer to these types as open ponderosa pine (Type 1), simple-structure Douglas-fir (Type 2), or complex-structure mixed grand fir (Type 3) based on the forest structure characteristics and tree species composition within each type.

The hierarchical mixed-effects model test for difference in breeding season use intensity across the three types showed that Barred Owls used the complex-structure mixed grand fir forest type more intensively than the open ponderosa pine or simple-structure Douglas-fir types (Table 5). Intensity of use did not differ across the forest types during the nonbreeding season.

DISCUSSION

The higher intensity of Barred Owl use during the breeding season within the complex-structure

mixed grand fir forest type relative to the other forest types was consistent with my expectation that closed-canopy stands with larger trees and more complex forest structure characteristics would be used more intensively by resident Barred Owls than open stands or stands with less structural diversity. As in Spotted Owls, this habitat selection pattern may be associated with characteristics that facilitate Barred Owl nesting, roosting, and foraging within these stands. For example, Wiens et al. (2014) and Hamer et al. (2007) both found that Barred Owls used structurally diverse old-forest cover types in greater proportion relative to their availability within their study areas in the Oregon Coast Range and North Cascades, respectively. Buchanan et al. (2004) reported that Barred Owls in the eastern Cascades nested in areas with greater diversity of tree species compared to surrounding areas, similar to the diversity of tree species in the complex-structure mixed grand fir type identified in this study.

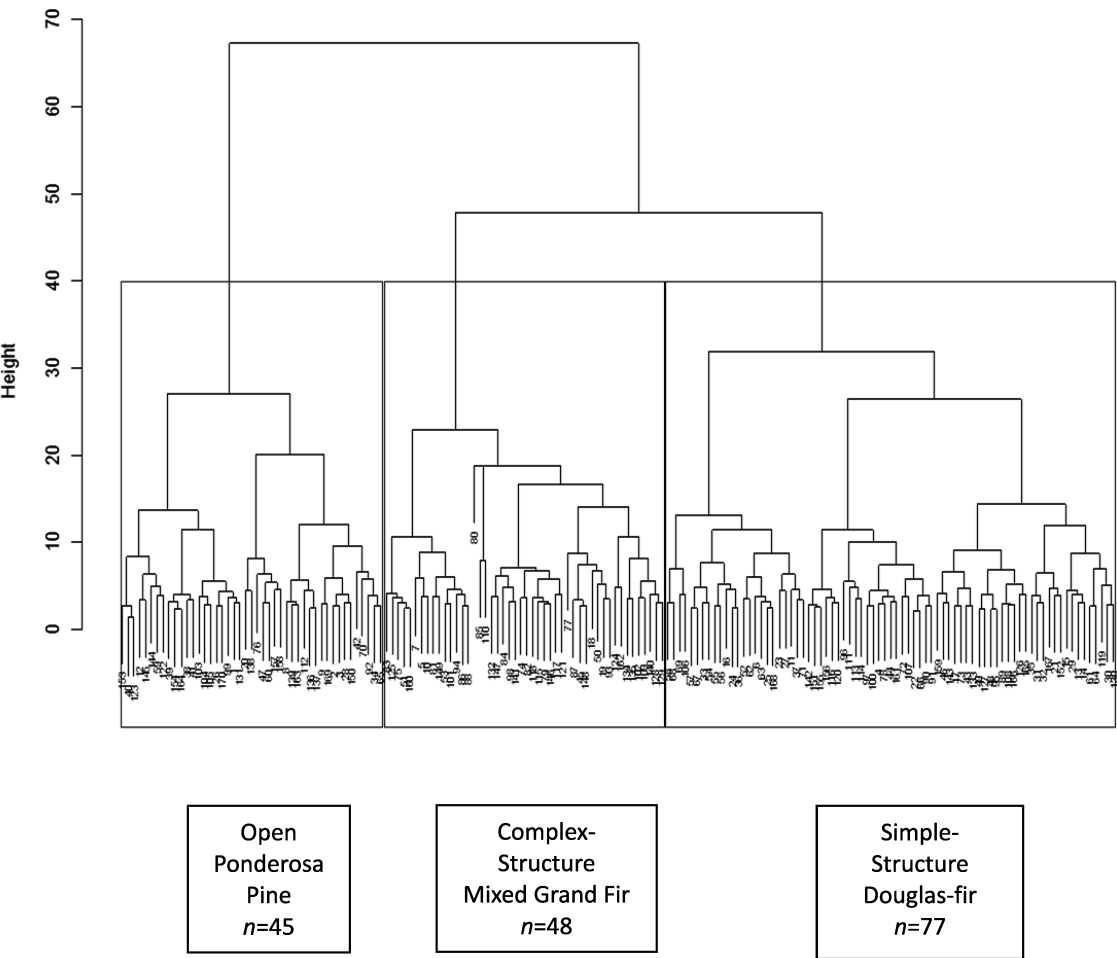


Figure 3. Hierarchical cluster analysis dendrogram showing three groups representing forest types found at plots within Barred Owl home ranges in the eastern Cascade Range, Washington.

Analysis of prey remains from Barred Owl pellets collected during this study indicated that Barred Owls captured prey commonly found on the ground (Graham 2012). The reduced ground cover within the complex-structure mixed grand fir stands may increase prey vulnerability and facilitate foraging on ground-dwelling prey species. The dense ground cover and open overstory canopy conditions in the open ponderosa pine type may be less suitable for Barred Owl use because of fewer foraging opportunities and greater vulnerability to predation by Great Horned Owls (*Bubo virginianus*) relative to the complex-structure mixed grand fir type. The simple-structure Douglas-fir stands notably lacked important forest structure characteristics (i.e., large trees, a structurally diverse canopy, snags, and logs)

that could be important for nesting, roosting, and foraging by Barred Owls.

I did not detect a difference in intensity of use across the three forest types in the nonbreeding season. There are two possible explanations for this. First, energetic requirements and behavioral patterns may have been different between the breeding and nonbreeding seasons. Barred Owls may have been more selective of habitat conditions during the breeding season when they were provisioning young and the young were highly vulnerable to predation. Barred Owls may function more as habitat generalists within their home ranges during the nonbreeding season. The second possible explanation is that the nonbreeding utilization distributions could reflect radiotelemetry sampling bias. Winter

Table 4. Mean and standard error of forest structure variables for three forest types identified within Barred Owl home ranges in the eastern Cascade Range, Washington. Column sample sizes indicate the number of plots assigned to each type.

FOREST VARIABLES	OPEN PONDEROSA PINE, TYPE 1 (n = 45)		SIMPLE-STRUCTURE DOUGLAS-FIR, TYPE 2 (n = 77)		COMPLEX-STRUCTURE GRAND FIR, TYPE 3 (n = 48)	
	MEAN	SE	MEAN	SE	MEAN	SE
COVER1	65.53	3.63	58.57	2.76	38.48	3.07
COVER2	46.71	3.47	39.88	2.87	37.04	3.13
COVER3	35.96	2.80	35.05	2.65	36.75	2.47
COVER4	33.96	3.57	47.43	2.11	59.48	2.75
LOGS	0.09	0.04	0.35	0.08	1.25	0.19
MTOE_PR	0.03	0.01	0.13	0.02	0.06	0.02
PR_ABGR	0.05	0.02	0.08	0.01	0.38	0.04
PR_PIPO	0.50	0.06	0.13	0.02	0.10	0.02
PR_PSME	0.28	0.05	0.72	0.03	0.31	0.04
SLOPE	15.24	1.64	16.77	1.21	12.67	1.57
SN_HA	3.93	1.18	9.19	1.66	32.74	3.89
SOLR	21.40	0.64	19.40	0.49	22.77	0.42
SW_DIV	0.46	0.05	0.67	0.05	0.87	0.05
TH_S2	34.05	6.32	20.67	2.32	31.31	3.02
TH_S3	39.29	6.15	78.20	5.01	73.88	5.47
TH_S4	12.01	3.26	41.97	3.80	57.30	5.97
TH_S5	0.00	0.00	0.26	0.18	4.91	1.87
TH_TOT	85.35	10.26	141.10	6.46	167.40	7.14
TR_HT_MN	15.76	1.09	25.41	0.62	27.40	1.05
TR_HT_SD	4.02	0.50	6.13	0.31	9.28	0.43
TR_ULC_MN	6.53	0.61	12.41	0.41	10.09	0.51
TR_ULC_SD	2.26	0.26	4.57	0.22	6.33	1.12

access to most of the Barred Owl sites required substantial over-snow travel by snowmobile and/or skis. Because of safety considerations, most (87%) of the locations used to calculate the nonbreeding season utilization distributions were daytime roosting locations. The nonbreeding season utilization distributions may reflect selection for daytime roosts that maximize solar warming, and may not adequately represent nocturnal foraging areas, because of these sampling patterns.

Although comparisons of forest structure associations for Spotted Owls and Barred Owls based on the information from this study and the literature on Spotted Owl habitat associations in the eastern Cascades is compromised by differences in study methods, such comparisons still provide useful insights. Forest structure characteristics associated with greater use by Barred Owls in this analysis were broadly similar to those used by Spotted Owls in the eastern Cascades (Buchanan et al. 1993, 1995, Ever-

Table 5. Mixed-effect, no-intercept model estimated utilization distribution value and 95% confidence intervals of that estimate for three forest types within Barred Owl home ranges in the eastern Cascade Range, Washington. Lower utilization distribution values indicate more intensively used areas.

FOREST TYPE	BREEDING SEASON			NONBREEDING SEASON		
	ESTIMATE	LOWER 95% CI	UPPER 95% CI	ESTIMATE	LOWER 95% CI	UPPER 95% CI
Open ponderosa pine	89.9	81.8	97.9	85.1	77.4	92.9
Simple-structure Douglas-fir	85.0	78.6	91.5	88.0	81.9	94.2
Complex-structure grand fir	69.0	62.2	75.8	85.6	79.1	92.1

ett et al. 1997, Sovern et al. 2011). Both species appear to be associated with similar tree species composition and stand structure characteristics. For example, on the eastern slope of the Cascade mountains, Spotted Owl nest stands occurred predominantly (92%) in grand fir or Douglas-fir forest series (Everett et al. 1997). King (1993) reported that Spotted Owl radiotelemetry locations were recorded most often in areas where a majority of trees were grand fir or Douglas-fir during her study on the Yakama Indian Reservation. Tree height diversity is also important relative to Spotted Owl habitat use in the eastern Cascades (Buchanan et al. 1995, Everett et al. 1997). In the eastern Cascades, tree height of dominant and codominant trees at Spotted Owl nest sites was 31.9 m (SD = 4.7) and canopy height of dominant trees was 15.4 m (SD = 4.3; Buchanan et al. 1995), similar to my measurements of mean tree height of 27.4 m (SD = 7.3) and live crown height of 10.1 m (SD = 3.5) at the complex-structure mixed grand fir plots. Ground cover and understory cover characteristics also appear to be similar for Spotted Owls and Barred Owls in this area. King (1993) reported that Spotted Owls preferred sites with understories characterized by litter or ferns and avoided those where small trees were abundant.

Although the forest structure associations for Spotted Owls and Barred Owls appear to be broadly similar, Spotted Owls in the eastern Cascade Range might be more closely associated with Douglas-fir dominated sites that have dense overstory canopy closure and abundant mistletoe clumps, whereas Barred Owls appear to be more associated with stands that have substantial numbers of grand fir trees and little mistletoe. For example, 92% of the Spotted Owl nests in the eastern Cascades were in Douglas-fir trees, and mean canopy closure at the nest sites was 75% (range 57–95%; Buchanan et al. 1993, 1995). Similarly, overstory canopy cover ranged from 83 to 94% at Spotted Owl nest sites in the eastern Cascades (Everett et al. 1997). King (1993) found that Spotted Owls were located more often in areas with high canopy closure (93.4%) compared to other areas within their home ranges (85.6% at random sites). These are all more densely closed canopy conditions than those found in the complex-structure mixed grand fir forest type associated with high levels of Barred Owl use in this study. In addition, Douglas-fir trees infected with dwarf mistletoe are an important habitat component associated with Spotted Owl nesting in the

eastern Cascades (Buchanan et al. 1995, Everett et al. 1997, Sovern et al. 2011). Within the Cle Elum Demography Study Area, 90% of 276 Spotted Owl nests recorded at 73 territories were on platforms, mostly in clumps of deformed limbs caused by dwarf mistletoe (Sovern et al. 2011). In contrast to Spotted Owl habitat associations in the area, increased abundance of dwarf mistletoe was not associated with increased intensity of Barred Owl use. In this study, dwarf mistletoe was most abundant in the simple-structure Douglas-fir forest type.

Landscape-scale characteristics, particularly slope and topographic position, are important for distinguishing between Spotted Owl and Barred Owl locations in the eastern Cascade Range, and may be more important than fine-scale forest structure (Singleton et al. 2010, Singleton 2013). Throughout the Okanogan-Wenatchee National Forest, slope was the most important characteristic for distinguishing between Spotted Owl and Barred Owl pair sites, and Spotted Owl sites in moderately steep mid-slope settings had higher occupancy probabilities through time compared to sites located in landscape settings preferred by Barred Owls (Singleton 2013). These patterns suggest that landscape-scale characteristics like slope and topographic position may be more important than fine-scale forest structure for identifying areas more likely to support Spotted Owls than Barred Owls, but these patterns are probably the consequence of competitive displacement of Spotted Owls by Barred Owls and may not provide for Spotted Owl population persistence over time (Singleton 2013).

Overall, the fine-scale forest structure conditions used by Barred Owls in this study broadly overlapped those reported for Spotted Owls in the eastern Cascade Range. Potential differences in fine-scale forest structure associations between the two species could reflect displacement effects where Spotted Owls have been displaced from the highest quality habitat as a result of competitive interactions with Barred Owls. Although these subtle differences are intriguing, they cannot be rigorously evaluated with the current data and should be considered hypotheses that remain to be tested. The findings of this study suggest that vegetation manipulation alone is unlikely to provide the basis for a strategy to mitigate negative effects on Spotted Owl populations resulting from competitive interactions with Barred Owls in mixed-conifer forests of the eastern Cascade Range.

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LITERATURE CITED

- BUCHANAN, J.B., T.L. FLEMING, AND L.L. IRWIN. 2004. A comparison of Barred and Spotted owl nest-site characteristics in the eastern Cascade Mountains, Washington. *Journal of Raptor Research* 38:231–237.
- , L.L. IRWIN, AND E.L. MCCUTCHEN. 1993. Characteristics of Spotted Owl nest trees in the Wenatchee National Forest. *Journal of Raptor Research* 27:1–7.
- , ———, AND ———. 1995. Within-stand nest site selection by Spotted Owls in the eastern Washington Cascades. *Journal of Wildlife Management* 59:301–310.
- COURTNEY, S.P., J.A. BLAKESLEY, R.E. BIGLEY, M.L. CODY, J.P. DUMBACHER, R.C. FLEISCHER, A.B. FRANKLIN, J.F. FRANKLIN, R.J. GUTIERREZ, J.M. MARZLUFF, AND L. SZTUKOWSKI. 2004. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, OR U.S.A. <http://www.fws.gov/oregonfwo/Species/Data/NorthernSpottedOwl/BarredOwl/Documents/CourtneyEtAl2004.pdf> (last accessed 28 July 2014).
- DUGGER, K.M., R.G. ANTHONY, AND L.S. ANDREWS. 2011. Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological Applications* 21:2459–2468.
- EVERETT, R.L., D. SCHELLHAAS, D. SPURBECK, P. OHLSON, D. KEENUM, AND T. ANDERSON. 1997. Structure of Northern Spotted Owl nest stands and their historical conditions on the eastern slope of the Pacific Northwest Cascades, USA. *Forest Ecology and Management* 94:1–14.
- FARAWAY, J.J. 2005. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall, Boca Raton, FL U.S.A.
- FORSMAN, E.D., R.G. ANTHONY, K.M. DUGGER, E.M. GLENN, A.B. FRANKLIN, G.C. WHITE, C.J. SCHWARTZ, K.P. BURNHAM, D.R. ANDERSON, J.D. NICHOLS, J.E. HINES, J.B. LINT, R.J. DAVIS, S.H. ACKERS, L.S. ANDREWS, B.L. BISWELL, P.C. CARLSON, L.V. DILLER, S.A. GREMEL, D.R. HERTER, M. HIGLEY, R.B. HORN, J.A. REID, J. ROCKWEIT, J. SCHABERL, T.J. SNETSINGER, AND S.G. SOVERN. 2011. Population demography of Northern Spotted Owls. *Studies in Avian Biology* 40:1–106.
- GRAHAM, S. 2012. Diet composition, niche and geographic characteristics, and prey size preference of Barred Owls (*Strix varia*) in the Pacific Northwest. M.S. thesis, Boise State University, Boise, ID U.S.A.
- HAMER, T.E., E.D. FORSMAN, AND E.M. GLENN. 2007. Home range attributes and habitat selection of Barred Owls and Spotted Owls in an area of sympatry. *Condor* 109:750–768.
- HERTER, D.R. AND L.L. HICKS. 2000. Barred Owl and Spotted Owl populations and habitat in the central Cascade Range of Washington. *Journal of Raptor Research* 34:279–286.
- HOOGE, P.N. AND B. EICHENLAUB. 1997. Animal movement extension to ArcView. Version 1.1. U.S. Geological Survey, Alaska Science Office, Anchorage, AK U.S.A.
- KING, G.M. 1993. Habitat characteristics of Northern Spotted Owls in eastern Washington. M.S. thesis, University of California at Berkeley, Berkeley, CA U.S.A.
- LILLYBRIDGE, T.R., B.L. KOVALCHIK, C.K. WILLIAMS, AND B.G. SMITH. 1995. Field guide for forested plant associations of the Wenatchee National Forest. Gen. Tech. Rept. PNW-GTR-359. U.S.D.A. Forest Service, Pacific Northwest Research Station, Portland, OR U.S.A.
- LIVEZEY, K.B. 2007. Barred Owl habitat and prey: a review and synthesis of the literature. *Journal of Raptor Research* 41:177–201.
- MARZLUFF, J.M., J. MILLSPAUGH, P. HURVITZ, AND M.S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Stellar's Jays. *Ecology* 85:1411–1427.
- MILLSPAUGH, J.J., R.M. NIELSON, L. McDONALD, J.M. MARZLUFF, R.A. GITZEN, C.D. RITTENHOUSE, M.W. HUBBARD, AND S.L. SHERIFF. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.
- OLSON, G.S., R.G. ANTHONY, E.D. FORSMAN, S.H. ACKERS, P.J. LOSCHL, J.A. REID, K.M. DUGGER, E.M. GLENN, AND W.J. RIPLE. 2005. Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. *Journal of Wildlife Management* 69:918–932.
- PEARSON, R.R. AND K.B. LIVEZEY. 2003. Distribution, numbers, and site characteristics of Spotted Owls and Barred Owls in the Cascade Mountains of Washington. *Journal of Raptor Research* 37:265–276.
- SINGLETON, P.H. 2013. Barred Owls and Spotted Owls in the eastern Cascade Range, Washington. Ph.D. dissertation, University of Washington, Seattle, WA U.S.A.
- , J.F. LEHMKUHL, W.L. GAINES, AND S.A. GRAHAM. 2010. Space use and habitat selection by Barred Owls in the eastern Cascades, Washington. *Journal of Wildlife Management* 74:285–294.
- SOVERN, S.G., M. TAYLOR, AND E.D. FORSMAN. 2011. Nest reuse by Northern Spotted Owls on the east slope of the Cascade Range, Washington. *Northwestern Naturalist* 92:101–106.
- U.S. FOREST SERVICE (U.S.F.S.). 2005. Forest inventory and analysis national core field guide. Vol. I: field data collection procedures for phase 2 plots. Version 3.0. U.S.D.A. Forest Service, Washington, DC U.S.A.

- U.S. FISH AND WILDLIFE SERVICE (U.S.F.W.S.). 2011. Revised recovery plan for the Northern Spotted Owl, (*Strix occidentalis caurina*). U.S.D.I. Fish and Wildlife Service, Portland, OR U.S.A.
- WIENS, J.D., R.G. ANTHONY, AND E.D. FORSMAN. 2014. Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in western Oregon. *Wildlife Monographs* 185:1–50.
- ZUUR, A.F., E.N. IENO, N.J. WALKER, A.A. SAVELIEV, AND G.M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY U.S.A.

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